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ORIGIN AND DEVELOPMENT OF THE LAMELLAE IN COPRINUS

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(WITH PLATES V–XII AND SIX DIAGRAMS)

Introduction

Members of the Agaricaceae thus far studied present two types in the origin and development of the lamellae. In one of these types,[1] which for the present we may speak of as the *Agaricus* type, the origin of the lamellae has been clearly described. It is preceded by the formation of a palisade layer of hyphae representing a young stage in the development of the hymenophore on the under side of the young pileus. This palisade layer of the hymenophore is either accompanied by, or, in many of the forms described, preceded by a more or less well developed, general, annular cavity. This cavity is, therefore, when present in the forms described, prelamellar. It is formed by differences in tension on the tissue

[1] In the following examples of the *Agaricus* type, the origin of the lamellae has been clearly described: *Agaricus carneotomentosus* (*Panus torulosus*) by HOFFMANN (**19**, p. 145); *Cantharellus tubaeformis*, *C. aurantiacus*, *Panus stipticus*, *Pleurotus tremulus*, *Omphalia umbellifera*, *O. pyxidata*, *Marasmius epiphyllus* by HOFFMANN (**20**); *Collybia velutipes*, *C. fusipes*, *Hygrophorus chlorophanus*, *Galera mycenopsis*, *Hebeloma mesophaeus*, *Coprinus fimetarius*, *Paxillus involutus*, *Entoloma sericeum*, and others by HOFFMANN (**21**); *Mycena vulgaris*, *Collybia dryophila*, *Nyctalis parasitica*, *Clitocybe cyathiformis*, and *Cantharellus infundibuliformis* by DEBARY (**14**, **15**, **16**, the latter two in conjunction with WORONIN); *Coprinus lagopus* by BREFELD (**12**, p. 127); *Agaricus campestris* by ATKINSON (**5**); *Hypholoma* by Miss ALLEN (**1**) and by BEERS (**11**); *Stropharia ambigua* by ZELLER (**23**); *Agaricus arvensis* and *A. comtulus*, and *Armillaria mellea* by ATKINSON (**6**, **7**).

of the young basidiocarp, due to the more rapid growth of the pileus and stem primordium, and the less rapid growth of the fundamental plectenchyma below the pileus primordium, in the angle between it and the stem. The fundamental plectenchyma is thus torn apart, and in those cases where this annular cavity is well formed prior to the origin of the palisade layer of the young hymenophore, the surface of the cavity is very ragged from the loose hyphae projecting to different distances in the cavity. This ragged appearance disappears over the roof of the cavity as the palisade layer is established.

The cavity and the palisade layer[2] first appear near the stem fundament. The pileus primordium is at this time comparatively limited in extent. The margin is younger than the portion next to the stem. As growth continues, there is centrifugal growth of the pileus at the margin, and this is accompanied by the centrifugal extension of the annular cavity, followed by the centrifugal extension of the palisade layer. In this way the elements are younger toward the margin of the pileus and older toward the stem.

In the forms described, belonging to this type, the lamellae originate in the form of downward projecting ridges or folds of the palisade layer. These ridges or folds begin at or near the stem, the newer, younger, radial extensions of them proceeding centrifugally; while the lamella increases in width downward by increase of the elements of its surface, and growth of the trama hyphae extending from the pileus above. The first evidence of a downward projecting ridge, or fold, which is the fundament, or early stage of the lamella, is the result of the increase in size and number of the elements of the palisade layer of the young hymenophore in a line radiating from or near the stem outward, or by the more rapid elongation of the trama hyphae of the young pileus along this line and next to the palisade layer, or by both processes combined. These elongating trama hyphae, as they pass into the gill salient, form the beginning of the trama of the lamella.

[2] FISCHER (**81**, p. 505) describes the origin of the young level palisade hymenophore, in *Armillaria mucida*, as growing inwardly toward the stem from the margin of the pileus, being a continuation of the palisade layer forming the surface of the pileus.

The second type in the origin of the lamellae has been observed in certain of the Amanitae, in *Amanita muscaria* by BREFELD (12), in *A. rubescens* by DEBARY (14, 15, 16), and in *Amanitopsis vaginata* by the writer (ATKINSON 10). Here the first evidence thus far observed of the origin of the lamellae is a series of bars or trabeculae, radiating from the stem outward, and attached to both the stem and the under surface of the pileus. These bars appear at first faintly differentiated. The tissue from which they are differentiated is evidently that which is formed by the growth of the primordium of the hymenophore from the under surface of the pileus toward the stem, apparently through the ground tissue of the young basidiocarp. There is no general, annular, prelamellar cavity, not even a weakly developed one. On the lateral surfaces of these radiating bars which are the fundaments of the lamellae, the hymenium is organized, the lamellae begin to separate more and more from each other, and gill cavities or chambers appear between them, while the lamellae are still attached to the stem.

Just how this growth of the hymenophore primordium advances through the fundamental tissue between the pileus and stem has not been as yet satisfactorily observed, and the same may be said of the organization of the hymenium on the lateral surfaces of the lamellae. It cannot, therefore, be stated at present to how great a degree this "*Amanita*" type differs from the "*Agaricus*" type.

In the forms thus far studied which represent the first type, or *Agaricus* type, the size of the general annular gill cavity often increases as the plant ages, and the gills are usually quite free from the stem up to maturity. Since in species of *Coprinus* the gills are attached to the stem at maturity, and separate from it during the later expansion of the plant and the shedding of the spores, the question arose during my study of *Amanitopsis*, as to whether the origin of the lamellae in such species of *Coprinus* was like that presented by the *Amanita* type or not.

Not only in *Coprinus*, but in other members of the Agaricaceae the origin of the lamellae presents, at this time, additional interest because in the July number of the *American Journal of Botany*, on the basis of a peculiar structure observed in *Coprinus micaceus*, the statement is made that one of the problems yet to be worked out in

the Agaricaceae is the origin of the lamellae (see LEVINE **22**); and this notwithstanding the fact that in a number of species several different persons have clearly and accurately described the origin of the lamellae.[3] It is further stated in the paper just referred to, after describing the peculiar structure observed in *Coprinus micaceus*, that "There is no general annular gill cavity as described by HOFFMANN, DEBARY, ATKINSON, and others, and no annular hymenial primordium" (LEVINE **22**, p. 352). Since DEBARY (**14**, p. 69) is the only person who has ever announced the existence of a general annular gill cavity in *Coprinus micaceus*, this ambiguous statement can be interpreted only as a denial of the existence of a general, annular, prelamellar cavity in *Agaricus campestris*, and other species of this genus, and other genera in which it has been described.

According to the peculiar situation said to precede the origin of the lamellae in *Coprinus micaceus* (LEVINE **22**), there first appear, isolated in the fundamental elements, radiating ridges of short converging hyphae. These ridges are said to split, and approximate halves of adjacent ridges unite to form the lamellae. It is also stated that there is no general palisade layer of the young hymenophore preceding the formation of the lamellae. So far

[3] HOFFMANN, more than half a century ago (**19**, p. 145), correctly described the origin of the lamellae in *Agaricus carneotomentosus* (*Panus torulosus*). The unequal growth of the young, even, palisade hymenophore gives rise to radiating folds which later become the lamellae. Later he observed the same method of origin in *Collybia velutipes* and more than a dozen other forms (**20**, **21**).

In DEBARY'S (**13**, pp. 386 and 394) first contribution to the origin of the gills, the palisade layer of the young hymenophore in *Nyctalis asterophora* and *parasitica* was said to present radial folds from its earliest appearance, that is, it was not a level or even layer. This interpretation of the early form of the hymenophore was shown by HOFFMANN (**20**, p. 402) to be wrong. The later study of a number of other forms, both gymnocarp and angiocarp, led DEBARY (**14**, p. 63; **15**, pp. 58 and 312; **16**, pp. 55 and 289) to the conclusion that the same course of development as described by HOFFMANN prevailed in most of the Agaricaceae. He now recognizes the earliest stage of the young palisade hymenophore to be level or smooth, even if only for a brief period. A very clear description is also given of the origin of the lamellae as downward growths of the young, level, palisade hymenophore along radial areas, commencing next the stem, progressing centrifugally, and broadening downward. An exception was made in the case of those forms with a true volva (*Amanita*, etc.). See the examples cited in the footnote on the first page of this article, in which the origin of the lamellae has been correctly described.

as the species of *Agaricus*, *Armillaria*, and *Lepiota* studied by the writer are concerned, it can be most positively reaffirmed, that, first, there is a general, annular, prelamellar cavity; second, a general palisade layer over the roof of this cavity precedes the origin of the lamellae; and third, the first radiating ridges or folds of the hymenophore are the fundaments of the lamellae themselves. The primary ridges or folds do not split to form the lamellae between them by the union of approximate halves of adjacent ridges. From the plants already studied, the writer has never formulated any generalizations as to what the situation may be in any other species or genera, in regard to the presence, either of a general annular gill cavity, of a palisade layer, or the origin of the gills. Without any bias, therefore, we may proceed to the interpretation of the situation in the three species of *Coprinus* which are the subject of the present paper.

Material

The material for study was collected in September 1914, all of it, with the exception of a few not very young specimens of *Coprinus atramentarius*, on the campus of Cornell University. It was fixed in chromacetic acid.

Coprinus comatus.—Two different collections were made of this species. The first lot of material was collected early in September in comparatively new made ground by the edge of a small bed of recently planted shrubs at the west end of Roberts Hall. A single plant had just emerged from the soil, and the aspect of the surroundings indicated that the colony was new and young. The mycelium was abundant and extended through the soil, partly in the cultivated portion, and partly in the newly made sod, for an area of less than 1 m. in extent; 20–25 young fruit bodies were collected from this area. The second lot of material was collected the latter part of September in a grassy plot east of Sage College. Here a number of mature plants had sprung up, but several very young ones were found scattered on the mycelium in the soil some distance from the old specimens.

The specimens were not growing in clusters, but scattered on the strands of mycelium. In the young material it was impossible

to observe external evidence of a differentiation into stipe and pileus. The plants were in the form of irregular tubercles, oval to elongate, the larger ones 1–1.5 cm. long by 3–5 mm. in diameter. Some of the larger ones in longitudinal freehand sections presented evidence of a differentiation in the upper part where the pileus and stem develop from the distal portion of the tubercle. When the material was microtomed and stained it was found that all stages were present, from a condition prior to any differentiation of the hymenophore up to quite an advanced stage of development, and often details of structure could be made out quite clearly by microscopic examination immediately after the paraffin ribbons were smoothed out on the slide.

Coprinus atramentarius.—The first material was collected early in September on the ground in a small park (Washington Park, Ithaca), but this material was not very satisfactory, since it was rather old and the compact soil was difficult to remove without damage to the fruit bodies. During the latter part of September some fine material was found growing on a very rotten stump on the campus quadrangle. The stump had been cut quite close to the ground, so that there was a sufficient amount of moisture, and yet the surface of the stump was free from soil except dust particles lodged from the air. The young fruit bodies were thus in an excellent condition for preservation, free from soil particles which might interfere with the knife in sectioning. There were several different clusters growing on this stump. The cluster which attracted my attention was about one-third grown, and careful examination in the rotten wood revealed several other clusters of very young fruit bodies from which the material was selected. In this species there is no large tubercle formed, but internal differentiation occurs when the basidiocarps are quite small, and oval or more or less pyriform in shape.

Coprinus micaceus.—This material was also collected from a very rotten stump on the campus quadrangle. Several years ago, as the elm trees were becoming too crowded on the campus, a large number were removed by thinning out the stand, the stumps being sawed off close to the ground. For several years enormous masses of this species have appeared on these stumps, and from their root

systems successive crops coming during rainy periods from spring until late autumn. While the fruit bodies usually appear in dense clusters, one can find clusters in different stages of development at almost any time during this season. From young clusters the basidiocarps of *C. micaceus* were collected.

I have thus gone into the details in regard to the collection of material for this study, in order to make it very clear that the basidiocarps grown in the open, under normal conditions, on their normal substratum, collected from young clusters, or scattered on the mycelium (*C. comatus*), were undergoing normal development. In these species it is fortunate that it is not necessary to grow them in the laboratory, upon artificial agar media, in order to obtain the young stages for study.

Study of Coprinus comatus

THE GENERAL, ANNULAR, PRELAMELLAR CAVITY.—It has not been the object of this investigation to study the origin and differentiation of the pileus and stem fundaments. The internal differentiation of these fundaments has taken place before the fundaments of the lamellae appear. The earliest stage yet studied in *C. comatus* is represented in fig. 1, from a section of the distal portion of a young basidiocarp, the great bulk of the tubercle having been removed. The young pileus is represented by the dark staining central zone, bordered above and on the sides by a distinct zone of radiating threads. The evidence appears to indicate that the system of radiating threads has its origin at the stem end of the tubercle as described by BREFELD (12) for *C. lagopus*, and that the fundament of the pileus proper is differentiated soon afterward. The outer zone of radiating threads is homologous with that which I have termed the blematogen (ATKINSON 8), and which BREFELD (12) calls the pileus volva ("Hutvolva"). But in *C. comatus* it remains "concrete" with the pileus, not separating from it as in the true or finished volva (*teleoblem*) of the Amanitae. Within the fundamental elements of this system of radiating threads, toward its center of origin, the pileus primordium becomes organized. The lateral portions, that is, the margin of the primordium, which is nearer the fundament of the hymenophore, appears to be differentiated

first, and this indicates that the primordia of hymenophore and pileus margin may arise from a fundament common to both. The further organization of the pileus consists in the growth of new elements, as well as in the incorporation of the elements of the inner zone of radial hyphae.

At the stage represented in fig. 1 there is no evidence either of an annular gill cavity or of the fundaments of the lamellae. The next stage in the differentiation of the basidiocarp is the appearance of a general, annular, prelamellar cavity. This is formed as a result of tensions due to unequal growth. The more rapid growth and expansion of the pileus fundament and the more rapid elongation of the stem fundament next the pileus bring into strong tension the less rapidly growing tissue in the angle between the pileus and the upper part of the stem, so that this tissue is torn apart. Prior to and at the time this tearing apart of the tissue occurs, the hyphae of the lower part of the pileus fundament are growing downward. When the rift first takes place the dome of this cavity, that is, the under surface of the exposed pileus fundament, is very irregular and "frazzled" from the numerous loose hyphae which project downward into the cavity, exactly as described for *Agaricus campestris* by the writer (ATKINSON 5). The lower surface of the cavity also presents in its early formation numerous loose hyphae on the surface of the stem and fundament of the partial veil.

The more active growth of the pileus, where the hyphae are richer in protoplasmic content and stain more deeply, is at some distance from the stem, near the outer portion of the annular cavity. It is along this under surface of the pileus that the palisade layer is first formed as the dome of the cavity smooths out and acquires a more even contour. At the extreme outer margin of the cavity, however, the surface is still irregular, due to the fact that the formation of the cavity and the organization of the palisade layer on the under surface of its roof are centrifugal, thus following up the centrifugal growth and extension of the pileus margin. The elements, therefore, not only of the pileus but also of the young hymenophore, are younger toward the margin of the pileus because of this centrifugal order of development.

It seems almost needless to state how the presence of a general, annular, prelamellar cavity is determined, when the fundamental principle of determining not only the extent, but the continuity and conformation of structure by serial sections, is so generally known; but inasmuch as the presence of such a cavity in the development of any of the Agaricaceae has been denied, it may be stated that its presence has been determined by serial longitudinal sections of basidiocarps, that is, sections parallel with the axis of the stem. Beginning on one side of the basidiocarp, as the sections enter the region of the annular cavity, there is but one cavity in each section which is more or less transversely elliptical in form. As the sections pass through the stem, there will appear two cavities symmetrically placed, one on either side of the stem; then as the sections pass beyond the stem through the opposite side of the basiodocarp, there is but one cavity, as on the entering side (see diagram I).

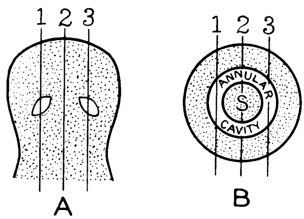

DIAGRAM I.—*A*, lateral view through young basidiocarp of *C. comatus;* longitudinal sections parallel with axis of stem, traveling from left to right; sections at *1* show single transversely elongated cavity; at *2* they would show two cavities symmetrically disposed, one on each side; at *3* they would show cavity similar to that in sections at *1; B*, zenith view through same, showing relation of sections to annular cavity at *1*, *2*, and *3;* see figs. 2, 3, 9, 10.

ORIGIN OF THE LAMELLAE.—*Coprinus comatus* is an exceedingly interesting form in which to study the origin of the lamellae. The "posterior" ends of the lamellae are not only "free" from the stem, but they are quite distant from it. In their origin, therefore, the question is not complicated by certain difficulties sometimes met with in studying the origin of lamellae which are "adnexed" or "adnate," or even where they are free at maturity but very close, or adnexed, to the stem in the very young stages. In *C. comatus* there is a circular area on the under surface of the pileus immediately surrounding the apex of the stem, over which the fundament of the hymenophore is not formed, at least in all the specimens which I have examined thus far. This accords with the earliest formation of the palisade layer, which, as previously stated, begins at some little distance from the stem and then proceeds

centrifugally. The origin of the lamellae begins on the earlier or older portions of the palisade layer of the young hymenophore, and likewise proceeds in a centrifugal direction.

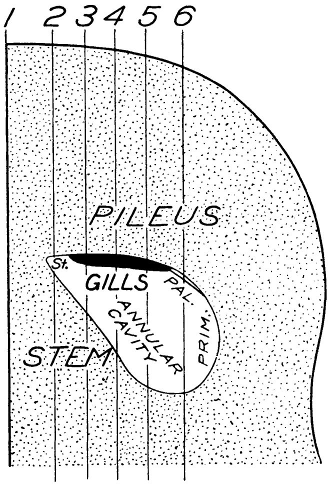

DIAGRAM II.—Lateral view through one side of basiodicarp of *C. comatus*, showing sectional view of annular cavity, and various stages in centrifugal development of young hymenophore; face view perpendicular to young gill; *st*, sterile area next stem; gills, broad black area; *pal*, palisade area; *prim*, primordial area before formation of palisade; a section at *1* would show structures as in face view of diagram (see fig. 11, opposite side); sections at *2* would show sterile area in middle (see fig. 15); sections at *3*, *4*, or *5* would show cross-cuts of young lamellae at middle (see figs. 13, 14); sections at *6* would show palisade area over middle and primordial area at each side (see fig. 12).

Since the lamellae thus originate at some little distance from the stem, on the lower surface of the roof of a well defined and relatively large annular gill cavity, their origin is determined with comparative ease. In the majority of the fruit bodies examined at the time of the origin of the lamellae, the area over which the first portion of the palisade layer extends and where the first salients, or fundaments, of the lamellae appear, is slightly convex and stands out nearly or quite perpendicular to the axis of the stipe. Sections parallel with the axis of the stipe, but tangential through this area, on either side of the stipe, cut the lamellae fundaments transversely and parallel with their, at this time, downward direction of growth (see diagram II, which illustrates the position of the sections). As the sections approach the stem on the near side, they gradually pass into the sterile circular area surrounding the stem. Through this field the sections show a middle area devoid of the salients. In passing through the stem a sterile area is presented on either side of the stem, but the origin of the lamellae is not so clearly observed here as in completely tangential sections, since the salients are cut in a strongly oblique direction, or parallel

with their axes (through or between them) in the median plane. Also, as the sections pass out of the stem, on the far side, the middle area is devoid of the salients, as on the near side, until the sterile area between the stem and young hymenophore has been passed.

In the tangential sections, therefore, far enough away from the stem to clear this sterile area, the salients over the middle portion are cut squarely in a transverse direction, while those on either side are slightly oblique, those at the extreme ends (sides) being slightly more so than those nearer the middle. But the salients are so small and narrow, and at this time extend radially to such a short distance, that it is very difficult, if not impossible, to appreciate the differences in the direction of the cut. At this earliest stage in the origin of the lamellae, the salients do not extend to the extreme margin of the cavity. From the area of salients there is a gradual transition in a centrifugal direction to the plain palisade area, and from this to the frazzled area at the extreme margin. For this reason the tangential sections through the area of the salients at this time show that the salients are confined to the middle portion, and the transition outward toward the margin on both sides passes into the palisade area and then into the frazzled area at the extreme margin (figs. 13, 15).

The first salients, or ridges, which appear in the young hymenophore are short, radial, downward projecting folds of the palisade layer. They are the fundaments of the primary lamellae themselves. They are formed by the increase and enlargement of the elements of the palisade layer along radiating lines. The increased pressure thus brought about in the palisade area causes a downward arching of these radial areas of the palisade, accompanied by the downward growth of the trama hyphae of the pileus along these radial areas; thus forming the trama of the young lamellae. The trama hyphae of the young lamellae are rather weakly developed, in contrast with the strong development of the hyphae of the palisade layer, being more slender, of less protoplasmic content, and forming a rather loose mesh.

The origin of the lamellae is very clearly shown in figs. 13–16. Fig. 14 is from a section just passing out of the sterile area on the

far side of the stem; fig. 13 is from a section just before passing from the area of salients to the palisade area; while fig. 12 is through the palisade layer beyond the gill salients. At either extremity of the series of salients in figs. 13 and 14, and on the left of fig. 16, it can be seen that the folds become less and less marked, finally presenting, as it were, only very slight undulations of the surface in the transition to the palisade area. These slight undulations, or salients, shown at the extreme ends of the series, are the distal ends of the lamellae fundaments. Tangential sections through a series of such radial salients which diverge slightly from a common center, and traveling from the stem toward the margin of the pileus, would pass through the distal ends of the salients on either side of the middle area before the ends of those over the middle area were reached (see diagram III). And, since the development of the pileus and the successive phases of the hymenophore are radial and centrifugal, the very low salients, or "undulations," are the very earliest stages in the origin of the lamellae fundaments. Fig. 16 is somewhat more highly magnified in order to bring out more distinctly the transition from the plain palisade phase of the hymenophore through the phase of weak salients to the more pronounced fundaments of the lamellae.

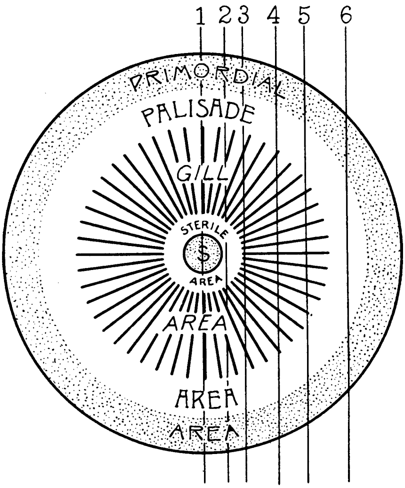

DIAGRAM III.—Zenith view through young basidiocarp of *C. comatus* at same stage as represented in diagram II; sections at *1* would be parallel with gills; at *2* they pass through sterile area, and gills on each side are cut obliquely (fig. 15); at *3*, *4*, and *5*, gills in median portion of sections cut transversely, those on each side obliquely; on each side of gills is palisade area, and centrifugal to this the primordial area (see figs. 13, 14); character of sections at *6* shown in fig. 12.

In some basidiocarps, at the time of the origin of the lamellae, or just prior thereto, the young hymenophore is relatively farther from the stem, and the plane of its surface, or rather a plane tangent

to its convexity, is not approximately perpendicular to the axis of the stem, but its outer portion is strongly depressed (see diagram IV), because the strong epinastic growth of the margin of the pileus causes it to curve downward. In such cases the sections, to be transverse to the salients and also parallel with their direction of growth, must be more or less strongly oblique to the axis of the stem. It can be seen readily that in such cases the young lamellae would be cut parallel with their direction of growth in width, only on one side of the basidiocarp, unless the latter had previously been cut into two longitudinal halves. Obviously this situation cannot well be determined in advance; but if entire basidiocarps are used, the situation can be interpreted, after cutting through the near side of the object, by an examination of the median sections parallel with the stem axis. The remaining half can then be oriented in such a way as to make the sections in the desired direction. If longitudinal halves of basidiocarps are used, however, a few sections can first be made on the stem side in order to determine the orientation of the young hymenophore.

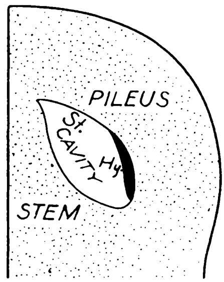

DIAGRAM IV.—Lateral view through one side of young basidiocarp of *C. comatus*, showing sectional view of annular cavity with surface of young hymenophore (*hy*) nearly parallel with axis of stem; *st*, sterile area next stem.

The further development of the lamellae consists in the radial extension of the salients originating in the downward folding of the palisade area, progressing in a centrifugal direction until the margin of the pileus is reached. The broadening of the lamellae, that is, their increase in breadth, is brought about not only by increase in size of the elements now present, and by continued growth of the trama hyphae of the young lamellae, but also by the increase in number of the elements of the hymenium and subhymenium throughout.

As the young basidiocarps become older, in order to obtain sections perpendicular to the origin of the lamellae, or parallel with their direction of growth, the cuts must be made more and more oblique to the axis of the stem, or finally perpendicular to it. This

results from the change in the relative position of the pileus during its growth, the pileus after a time approaching a position nearly or quite parallel with the axis of the stem. Figs. 23 and 24 are from sections perpendicular to the stem axis.

ATTACHMENT OF THE LAMELLAE TO THE STIPE.—Before the plants are fully mature the margins of the lamellae become attached to the stipe. The age of the lamellae when this attachment takes place probably varies in different plants, and even in the same plant, depending on the size of the annular gill cavity and the distance which the lamellae must grow in width before the margins come in contact with the stipe. For example, in some cases the younger portions of the lamellae at the extreme margin of the pileus may become attached to the stem before the older portions do, because of the narrower space between the margin of the pileus and the stem and the cramped situation in which the lamellae are immediately following their origin or at the time of their origin. Where the gill must cross an open space before it comes in contact with the surface of the stipe, the edge is evenly rounded and furnished with the closely parallel clavate cells forming the palisade layer which is continuous with the similar palisade layer on the sides forming the hymenium. When the lamellae come in contact with the stipe they press more and more firmly against it as growth continues. This pressure tends more and more to spread many of the palisade cells of the margin laterally, and thus bring the trama cells more or less in direct contact with the surface of the stem. This is well shown in fig. 23, where the three lamellae show different phases of this process. The one at the left shows the strong spreading of the marginal palisade cells with trama hyphae in contact with the stem. In the middle one the marginal cells are only partially spread, there being in this section two clavate cells which still keep the trama hyphae separated from the stem surface. In the lamella at the right the marginal cells have only just begun to spread laterally.

While the marginal cells of the lamellae are thus spreading laterally, and afterward, a few of these cells as well as branches from the trama hyphae, by growth, interlace more or less with the loose open plectenchyma of the stem surface and the junction is

thus effected. Because of the changing tensions to which the plant is subject more or less during growth, the lamellae may likely come in contact with the stem, the edges become more or less flattened out, then become free, and then again come in contact with the stem surface, and finally make the connection permanent, until expansion of the plant begins at maturity. In fig. 24 the lamella at the right, which had crowded slightly into the surface of the stem, and whose marginal cells are only slightly spread, has been slightly withdrawn from the stem during the smoothing out of the paraffin ribbon.

As the lamellae become more firmly crowded against the stem, the portion in direct contact loses the deep staining quality which the marginal palisade cells in common with the palisade cells of the hymenium on the sides possess. This is due to the fact that the greater part of the marginal palisade cells are squeezed out laterally, while the few which remain take on a more vegetative function, and, with the new growth of the trama hyphae here, form the interlacing and rather loose connection with the stem.

There is another interesting feature in the origin and development of the lamellae which requires a clear exposition, because it is present not only in the three species of *Coprinus* treated here, but also in the vast majority of the agarics, and perhaps with very few exceptions in all. Unless clearly analyzed, the situation might be misleading and result in an incorrect interpretation of the origin of the gills. The situation is presented in fig. 20, where the gills both to the left and right show the trama distinctly continuous with the tissue above and below. This situation may, and does often, occur even in quite young phases of the origin of the lamellae. This figure is of a tangential section parallel with the axis of the stem but near the margin of the pileus. Epinastic growth of the pileus margin causes it to curve in more toward the stem. Since the lamellae originate as radial salients on the inner side of the pileus and grow in breadth perpendicular to the surface of their origin, sections parallel with the axis of the stem but through the margin of the pileus would be parallel to a tangent of the pileus curve in this region. When the sections are made with the knife traveling from the stem through the far side of the basidiocarp, at the extreme left

and right of the hymenophore the sections will soon begin to present this relation of the lamellae (if the hymenophore is sufficiently advanced in age) even before the middle portion of the sections has reached the margin of the pileus. This is the situation presented in fig. 20. As the middle of the sections pass through the margin of the pileus (when the fertile portion has been reached), all of the lamellae will show the trama continuous with the tissue below as well as above (figs. 21 and 22). The attachment of the gills with the tissue "below" in the sections is at their point of origin from the *inner* surface of the pileus, exactly as in their attachment above. The sections under such conditions merely present the situation of the trama of the lamellae being continuous with the trama of the pileus at their point of origin. The connection "below" in such cases is not with the tissue of the stem, but with that of the pileus. Great care is necessary to avoid confusing such situations with those in which the gills become attached to the stem, for both situations may occur in the same sections. Diagram V illustrates the position, form, and relation of parts, and direction of the cut in obtaining the sections for figs. 20–22.

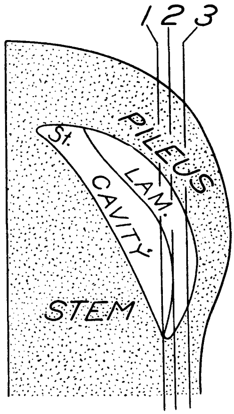

DIAGRAM V.—*C. comatus:* lateral view through one side of medium aged basidiocarp, showing sectional (cross) view of annular gill cavity, side view of lamella, epinastic curvature of pileus and hymenophore; in sections at *1*, *2*, or *3* gills will be free from stem in all cases; their free margins will show in middle of sections at *1*, but those on each side will be cut parallel with surface of pileus, and will show attachment both "above and below" to pileus at point of their origin (see fig. 20); sections at *2* and *3* will show all gills attached both "above and below" to pileus at their points of origin; sections here run through dorsum of gills (or near) and parallel with surface of pileus (see figs. 21, 22).

Study of Coprinus atramentarius

The youngest specimens of *Coprinus atramentarius* studied were in the phases of development just prior to and during the origin of the lamellae. No attempt has yet been made to study the earlier stages presented by the earliest differentiation of the pileus and stem, since the primary object of

the present study has been the origin and development of the lamellae. In the earliest stages examined the fundament of the pileus was distinctly organized, especially the marginal and lower portion. It is organized within the zone of radiating hyphae characteristic of many species of *Coprinus* which have been studied. The zone of radial hyphae external to the pileus is broad. It forms the blematogen, and is not separated as a distinct free volva or teleoblem, since it remains concrete with the surface of the pileus. The relation of the pileus and blematogen is very well shown in figs. 26, 27, and 38.

THE GENERAL, ANNULAR, PRELAMELLAR CAVITY.—In contrast to the pronounced and distinct annular gill cavity in *C. comatus*, the annular cavity in *C. atramentarius* is weak, often very weakly formed, but it was, nevertheless, present in all specimens examined. Since it is formed as a result of the tensions caused by difference in the rate of growth of the pileus, stem, and adjacent tissue, as described for *C. comatus*, *Agaricus campestris*, etc., the tissue underneath the pileus fundament and surrounding the stem is torn apart. Since the cleavage, as already described for *C. comatus*, *A. campestris*, etc., is not an even one, the tissue "shredded" more or less, so that free ends of hyphae project into the cavity from below and above. But since the cavity is here a weak one, there are scattered hyphae which have not become severed, but extend across the cavity from above downward or vice versa.

THE PALISADE LAYER OF HYPHAE.—The palisade layer of hyphae is present at this time, or even earlier, but the hyphae at first are slender. In the development of the pileus within the system of radiating threads, the hyphae on the margin and on the under surface which form the fundament of the hymenophore are parallel and rather closely compacted, so that the young fundament of the hymenophore has a palisade structure even before the tearing apart or shredding of the fundamental plectenchyma below, into which the hymenophore is progressing by growth. This fundament of the hymenophore stains more deeply than the fundamental plectenchyma below, or the pileus above, or the enveloping blematogen (figs. 26–35).

ORIGIN OF THE LAMELLAE.—The first evidence of the origin of the lamellae are radial salients of the hymenophore fundament, just described, which project downward (figs. 28, 31, 32, 34, 35, and 37). These salients are formed not only by the more rapid increase of the elements of the palisade layer but also by the elongation of the subadjacent trama cells of the pileus which support or bear them. The continued growth of these trama cells gives rise to the trama of the lamellae. In the early stages of the origin of the lamellae there is a striking difference in the character of the trama cells in *C. atramentarius* and those of *C. comatus*. In *C. comatus* the rather weak development of the trama hyphae in the very young lamellae, and the rather open mesh which they form, contrasts strongly with the compact tissue formed by the elongation of the trama extending from the pileus into the young gill salients of *C. atramentarius*. The compactness of the trama tissue at this time, together with the evidence of the elongation of its cells in the direction of the growth of the salients, gives the impression that this is a factor in the origin of the salients, which assists in thrusting or shoving downward the palisade tissue along the radial areas on which the young lamellae arise. The elongation of these trama cells of the pileus, subadjacent to the salients, is recognized not only by the form of the cells, but also from the fact that they stain less deeply than the intervening trama cells of the pileus subadjacent to the hymenophore (figs. 32 and 37).

Figs. 27–32, 34, and 35 are from the same basidiocarp, the sections all being parallel with the axis of the stem. Fig. 27 is from a median section; fig. 28 is tangential on one side where the young gill salients are quite distinct; fig. 29 is from the opposite side of the basidiocarp where the young hymenophore is still in the palisade condition before the appearance of the salients; fig. 31 is from the gill side, but nearer the margin of the pileus; and fig. 32 is the same more highly magnified. Fig. 34 is from a portion of the same, still more highly magnified to show the details of the palisade layer with the very earliest evidence of gill salients, 3 of which are shown. Fig. 35 is from the area of fig. 34 including the middle salient but still more highly magnified. In both figs. 34 and 35 the palisade layer of cells is very clearly shown, particularly so in fig. 35. The

palisade layer clearly extends over the young salients and is continuous with the palisade layer between them. The loose hyphae of the shredded fundamental plectenchyma connect indifferently with the palisade layer of the salients or with the palisade between them. Fig. 33 is from a tangential section of another basidiocarp, in which there was no evidence of the gill salients. The young hymenophore is in the even palisade stage with loose hyphae of the torn fundamental plectenchyma crossing the weak, general, annular gill cavity.

Thus from the very earliest evidence of the gill salients, when they can just be observed as projecting slightly below the level of the palisade hymenophore, it is readily seen that the more or less isolated hyphae, which retained their connection between the hymenophore above and the fundamental plectenchyma below, on the surface of the stem, and thus cross the weakly developed general gill cavity, are connected, some with the young salients, or gill origins, and some with the portions of the hymenophore between the salients (figs. 34, 35, and 37). This is very clear evidence that these hyphae of the fundamental plectenchyma, isolated during the formation of the gill cavity by the tearing apart or shredding of this tissue, have no formative or structural significance in the origin of the lamellae. As the lamellae increase in width they soon begin to press against the fundamental plectenchyma over the stem below. Their increase in width thus serves to carry the portion of the hymenophore between adjacent lamellae farther from the stem, and the isolated hyphae previously mentioned, which were connected with this portion of the hymenophore, are torn free.

The angle which the young hymenophore makes with the stem varies in different plants. In some it is perpendicular to the axis of the stem, that is, it stands out at right angles to the stem, as in fig. 27. In others it may be oblique, rising at an angle as shown in fig. 26. Sections of some fruit bodies were made oblique to the axis of the stem in the hope of obtaining some perpendicular to the young hymenophore where it rises at an oblique angle from the stem. Figs. 36 and 37 are from such sections of a basidiocarp during the early stages of the origin of the gills. The general gill cavity, though weak, is very clearly shown with its shredded

fundamental plectenchyma. In fig. 36, which is from near the margin of the young hymenophore, in a few places very slight salients are shown, but the lighter colored trama tissue is seen slightly projecting into some of them. Fig. 37 is from a section nearer the stem, where the salients have reached their greatest development in this particular basidiocarp. Here some of the salients are quite pronounced, but the palisade layer is continuous over and between them. There is no continuity of the trama of the pileus through the salients with the fundamental plectenchyma below, but the loose threads of the shredded fundamental tissue below connect indifferently with the margin of the salients or with the portions of the hymenophore between them. In the figures just cited and also in figs. 34 and 35 it is very clear that the first salients, or ridges, of the hymenophore are the fundaments of the lamellae themselves. They do not split, and approximate halves of adjacent ridges unite to form the lamellae, as has been said to be the case in *C. micaceus* (LEVINE **22**).

ATTACHMENT OF THE LAMELLAE TO THE STEM.—Since the gill cavity is weak, the lamellae become attached to the stem at quite an early stage. At or near maturity they are quite firmly attached to the stem, or the fundamental plectenchyma surrounding the stem, the edge of the lamellae for its entire thickness being very closely and compactly pressed against the surface of the stem, while the hyphae from both structures are more or less interlaced. A rather loose floccose layer of fundamental plectenchyma clothes the young stem, to which the lamellae become attached. This loose layer of irregularly interwoven hyphae is present in the mature plants, but becomes more compacted, probably because of the pressure to which it is subjected between the lamellae and stem. As the plants age, this zone of fundamental plectenchyma clothing the stem contrasts strongly with the stem structure, as seen in figs. 43 and 44.

The loose shredded character of this fundamental plectenchyma in the young basidiocarps is very favorable for the interlocking with it of the slender hyphae which grow out from the edges of the young lamellae. This interlocking of hyphae is shown in figs. 41 and 42, which represent different stages. The slender hyphae on the edge of the lamellae, pushing their way into the mesh of the

fundamental tissue, is well shown. The connection of the lamellae with the stem is still frail in these stages of development, and the distinctness of the lamellae as independent structures is very evident when considered in relation to the first salients which appear on the under surface of the hymenophore.

In the older stages the edges of the lamellae become so firmly pressed against the stem that the round edge is somewhat compressed, as shown in figs. 43 and 44. The hyphae on the extreme margin, which stain deeply in the younger stages where the connection with the stem is loose, are now crowded to one side or have lost their rich protoplasmic content, which now resides in the cells of the hymenium, with the exception of the cystidia. In order to free the lamellae from the stem, one preparation was purposely overheated in smoothing out the paraffin ribbon. The result is shown in fig. 44. In some of the lamellae the palisade layer of cells, at the point where this section was made, still extends entirely over the margin in the position which they occupied at an earlier period. In others these palisade cells have been crowded to the side. Either one or the other situation may occur on the same lamella at different points, according to location of the section, since the edge of the lamella varies throughout its length in this respect.

DECEPTIVE APPEARANCE OF SECTIONS WHERE THE FUNDAMENT OF THE HYMENOPHORE EXISTS ALSO AROUND THE UPPER END OF THE STEM.—Where the fundament of the hymenophore extends for a short distance down around the upper end of the stem, a situation is presented which may lead to error in the interpretation of the origin of the lamellae. Tangential sections parallel with the axis of the stem (or slightly oblique) made very close to the upper end of the stem present a very deceptive appearance. Such a section is shown in fig. 40, and perhaps represents a situation similar to that presented by LEVINE (**22**) in his figs. 13 and 14, pl. 39, of *Coprinus micaceus*. Such sections, even at a much younger stage, could very well give the impression that the trama of the gills at this time consisted of fundamental elements connected both with the pileus and stem; that the ridges or pockets between them gave rise to the hymenium, the latter structures splitting along a median line and approximate halves of adjacent ridges or pockets uniting to

form the gills. An examination of this situation, however, shows that, since the fundament of the hymenophore descends a short distance on the stem, when the first salients of the primary lamellae arise, they are present on the stem and continue over the angle on the under surface of the pileus. As these salients broaden into the young lamellae, little "stalls" or pockets lie between them in the angle between the apex of the stem and pileus. Longitudinal sections in this region will cut across the "stalls," and at this stage, when the stem surface slopes outward strongly, will be parallel to a tangent of the curved or angled lamellae, and will show the attachment of the trama not only to the pileus above but to the stem below. Such sections are perpendicular to the origin and direction of growth of the lamellae. Diagram VI illustrates the situation in question. Plants with adnate or decurrent lamellae are very favorable subjects for obtaining such deceptive sections. As stated previously, therefore, *C. comatus* is a very favorable object for studying the origin of the lamellae, since the gills in all stages of development are so distant from the apex of the stem. A situation similar to that represented in fig. 40 may even be presented by species with "free" gills, since there is often variation in individuals in respect to "free" or "adnexed" gills. In another paper I shall show that the same situation is present in some individuals of *Agaricus rodmani*.

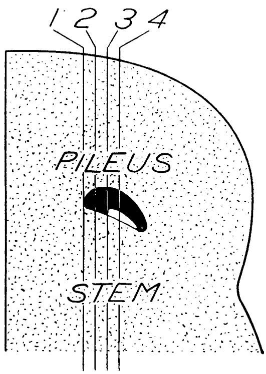

DIAGRAM VI.—Lateral view through one side of young basidiocarp of *C. atramentarius* with "adnate" gills; gill origins extend down on apex of stem, leaving little "stalls" or pockets between them in angle between apex of stem and pileus; sections at *1*, *2*, and *3* are across these "stalls" but through *gill origins* both "above and below" (see fig. 40).

CYSTIDIA.—No special effort has been made to study the cystidia, but their presence and relation in sections of medium and nearly mature plants was so striking as to excite interest and some observation. When the lamellae are quite well advanced, but still moderately young, the cystidia are quite numerous and

very close together in the hymenium, as shown in fig. 42. At this stage of development the approximate hymenia of two adjacent lamellae are still more or less separated, showing distinct gill chambers, but the numerous cystidia already project above the level of the young basidial hymenium. At certain places two cystidia from opposite hymenia meet head on and the pressure sometimes results in a deformity of one or both. Even at this stage of development it can be seen that many of the cystidia originate below the subhymenium. In this respect my observations do not agree with those of BULLER (**12a**), who describes and figures the cystidia of *C. atramentarius* as arising from the small subhymenial cells at the same level as the origin of the basidia.

In older stages of the lamellae (figs. 44 and 45) the approximate hymenia of adjacent lamellae become very closely crowded together, so that the gill chambers are entirely obliterated. The hymenia are very compact and deeply stained, while the trama presents a loose open mesh and is lightly stained. One of the striking features at this stage is the appearance of the cystidia in cross-sections of the gills. With low magnification they appear as quite regularly spaced clear areas, oblong or elliptical in outline, lying directly across the two approximate hymenia. With low magnification it is often difficult or impossible to determine from which lamellae a given cystidium originates. With higher magnification one can readily determine the lamella from which they arise. Now it is very clear that many of them, at least, originate from hyphae of the trama below the subhymenium. I have not examined the situation thoroughly enough to make any general statement. It is possible that some of them may arise from subhymenial cells on a level with the origin of the basidia, as BULLER states, but it is very certain that many of them originate in the trama. In fig. 45 a cystidium is shown which originates from the middle of the trama.

During the growth of the cystidia they push their way into the hymenium of the adjacent lamella, according to my observations, much farther than illustrated by BULLER. The one shown in fig. 45 has pushed through the hymenium of the adjacent gill. Many of them reach this distance and some even extend into the

subhymenium or trama. As BULLER has stated, their hold upon the adjacent lamella is so strong that it is difficult or impossible to separate the lamellae without tearing. In an endeavor to separate the lamella in the paraffin ribbon at the stage of development shown in fig. 45, while smoothing it out on the slide, I have tried overheating the ribbon. In all cases the lamellae were torn open through the trama, the adjacent hymenia remaining as firmly bound together as ever. While at this stage of development the adjacent hymenia are in close contact so that the gill chambers are obliterated, at the time of shedding the spores the lamellae are spaced and the gill chambers are again apparent. The moving apart of the gills is very likely brought about by the elongation of the cystidia, for they are very much longer at maturity than at the stage shown in fig. 45.

Study of Corprinus micaceus

The very young basidiocarps are oval or oboval in form. In the youngest ones sectioned, the young lamellae were already present as slight salients of the hymenophore extending from the stem outward to near the young hymenophore margin. As shown in figs. 46–49, the relation of the pileus and blematogen is of the *Coprinus* type, the blematogen covering the pileus consisting of radiating hyphae whose cells have swollen mostly into globose forms. As they age the hyphae fall apart, forming a more or less powdery material which adheres in small flocculent masses or flakes, and in the light glisten to such an extent that they have suggested the glistening of mica flakes, which easily fall away by friction from foreign substances.

FORMATION OF A PALISADE LAYER ON THE OUTER SURFACE OF THE PILEUS.—At quite an early stage in the development of the pileus, the hyphae on the upper surface grow in an irregularly radial direction within the inner portion of the blematogen. This can be seen in basidiocarps of the stage presented in fig. 68, which is a somewhat more highly magnified photomicrograph of a section from the same basidiocarp as fig. 46. On the surface of the pileus can be seen faint indications of the radiating, more deeply stained, hyphae. In a slightly older stage (fig. 69) they form a more com-

pact even layer. In fig. 70, from a still older basidiocarp, it can be very clearly seen that the surface hyphae of the pileus form a compact palisade layer below the zone of large blematogen cells, though the ends of the hyphae are not yet aligned into such an even surface as they present later. Many of these hyphae represent new growth and branching of the earlier elements of the inner, but not well defined, zone of radiating threads, and possibly some of these older elements are incorporated in the palisade layer. Whether any of them take part in the formation of the mature palisade by abscission of the distal portion at the level of the palisade surface, however, or whether all are compressed between the broadening cells of the forming palisade and are thus merely pinched off, as stated below, has not been determined. The incorporation of some of the older hyphae into the palisade does not seem improbable.

The surface of the pileus is already beginning to show the strong folds with intervening depressions ("striations") over certain of the older lamellae, which is clearly presented in the nearly, or quite, mature plant. At the completion, or maturity, of the palisade layer on the outer surface of the pileus, the cells are clavate, very closely packed side by side, the free ends slightly convex or nearly truncate (fig. 71). In this figure the broad folds with the narrow intervening depressions are clearly brought out in cross-section, the depressions, or "striations" as they are called, correlated in their position with the trama of the older, or primary, gills, so characteristic a feature of many species of *Coprinus*.

SHEDDING OF THE BLEMATOGEN LAYER.—In the shedding of the blematogen layer the greater part of the mass of rounded cells is freed by the frail connection between the cells, perhaps due to a weakening of the middle lamella accompanied by the rounding of the cells and constriction between them. The chains of rounded cells are formed on filaments of a few slender cells, some of which project from between the cells of the palisade layer (a few can be seen near the middle of fig. 69). As the palisade layer approaches maturity, the crowding of the cells into the compact layer very probably pinches off these slender supporting hyphae. A thorough study of the shedding of the blematogen has not been made, but it

is clear that the process is different from that which occurs in *Amanitopsis vaginata* (see ATKINSON **10**) and *Amanita volvata* Peck, where the outer surface of the pileus primordium, by gelatinization, or other means of disintegration in *A. volvata*, forms a cleavage layer, thus freeing the blematogen, which then becomes the volva or teleoblem. In *Amanita muscaria* a similar cleavage layer is formed by gelatinization of the outer layer of the pileus, as described by BREFELD (**12**, p. 125).

The method of separation of the blematogen from the pileus in *C. micaceus* is different, therefore, from that in the species of *Amanitopsis* and *Amanita* just mentioned, and very likely in many other species of *Amanita* which as yet have not been studied in respect to this feature. The method of separation of the blematogen in other species of *Coprinus* and *Amanita* should be examined, particularly viscid species of *Coprinus*, and species of *Amanita* with a dry powdery volva. In some of the latter the pileus is viscid when fresh, and it is likely that a cleavage layer is formed by the gelatinization or other method of disintegration of the outer layer of the pileus.

THE GENERAL, ANNULAR, PRELAMELLAR CAVITY.—The general annular gill cavity in *C. micaceus* is formed in the same way as described for *C. atramentarius*. It is also weakly developed as in that species. The tensions resulting from the differences in growth tear apart and shred the ground tissue immediately below the fundament of the hymenophore. Scattered threads here and there extend across the cavity, connecting with the palisade layer of the hymenophore fundament not only at points where the first salients of the lamellae arise but also between them.

ORIGIN OF THE LAMELLAE.—Since the organization and development of the fundament of the hymenophore and of the lamellae origins proceed in a centrifugal direction following the centrifugal growth of the pileus margin, the presence of the palisade layer of the hymenophore fundament, as well as the origin of the lamellae, can be observed near the margin of the pileus in tangential sections parallel with the axis of the stem. The older stages of the gills can then be traced in the serial sections passing up to the stem. The youngest basidiocarp studied is represented in longitudinal

section through the stem (parallel with its axis) in figs. 46 and 47. Fig. 46 is from a section near the middle of the stem, while fig. 47 is near the surface of the stem at its junction with the hymenophore, but still including a considerable portion of the stem at this place. The young lamellae in fig. 47, therefore, are cut somewhat obliquely, but the margins present their relative position in relation to the gill cavity and the fundamental plectenchyma below clothing the stem.

Four serial sections beginning near the margin of the hymenophore and traveling toward the stem are shown. Fig. 52 is near the margin of the young hymenophore, and shows not only the palisade layer of the same but the general gill cavity preceding the origin of the lamellae. In fig. 53 the first evidence of the salients or fundaments of the lamellae are seen, resulting in a slight undulation of the palisade surface of the young hymenophore. A few of the stray hyphae extending across the general gill cavity are connected with some of the gill salients, while others are connected with the portion of the hymenophore between the salients. Above a few of the salients the hyphae of the trama are lighter colored because of their lessened protoplasmic content resulting from their elongation, which assists in pushing down the salient. In fig. 54 the salients or ridges are still more prominent. Portions of loose threads from the shredded fundamental plectenchyma below are loosely connected with some of the salients, and others with the palisade portion of the hymenophore between them, especially the younger portions at either side of the section. Fig. 55 represents a still older stage of the young lamellae. In this section the margins of the lamellae show a feature which is quite characteristic of the very young lamellae of *C. micaceus*. This is the lateral spreading or fan-tailing of the margin, caused by the outward curving of the hyphae, and particularly by the swelling of the marginal cells into subglobose or pyriform bodies, which is probably largely responsible for this fan-tailing of the young gill margins. These swollen cells form cystidia.

As the lamellae become broader they press more and more upon the loose fundamental tissue beneath. The swollen cells on the margin of the young lamellae, pressed against the loose tissue

below, simulate fundamental elements, and if care is not used in searching for younger stages of the lamellae, might easily lead one into error in the interpretation of their origin. All of these features are more strongly emphasized in figs. 56–63, from an older basidiocarp, which represent somewhat older stages of development of the lamellae. The lighter coloring of the trama, the fan-tailing of the lamellae, and numerous swollen cystidia on and near their margins are very clearly shown. At this stage of development one might be misled as to the true origin of the lamellae unless the origin of these structures was sought in earlier stages.

From a study of the situation presented by these figures it is very clear that the first salients, or ridges, on the under side of the pileus, are from the young hymenophore palisade layer, just as they are in *C. comatus* and *C. atramentarius* previously described. The first ridges which appear are the fundaments of the lamellae themselves. They do not arise as isolated ridges of cylindrical or clavate cells, in the fundamental plectenchyma, and then split, the halves separating and those of adjacent ridges then uniting to form the gills, as described for *C. micaceus* by LEVINE (**22**). The photomicrographs represented in his figs. 13 and 14 present very strong evidence of being sections through the adnate portions of the lamellae close to the stem, as I have already described for *C. atramentarius* and represented in fig. 40. At this stage in the development of the basidiocarp, the outer surface of the stem is strongly oblique or nearly horizontal, and several serial sections in this region would present the appearance shown in the figures in those cases where the gill origins are on the apex of the stem as well as on the under side of the pileus. At any rate, these figures represent an old stage in the development of the lamellae, and if this peculiar structure had been traced to its origin, the origin of the lamellae would have been found. Even if there were no general, annular, prelamellar cavity formed in certain individuals, or if it should be insisted that the weak cavities where, in the shredding of the ground tissue, some scattered hyphae or loose strands extend across, are not general, annular, prelamellar cavities, the first ridges or salients to appear are nevertheless the fundaments of the lamellae; in other words, they are the gill origins. BREFELD was

right when he said in regard to the origin of the lamellae of *C. lagopus* that they arise as new, free vegetation points on the under surface of the pileus and continue through apical growth (**12**, p. 127). It should be said, however, that growth continues throughout the width of the lamellae and of the palisade layer.

Besides the clear evidence just presented as to the origin of the lamellae in *C. micaceus*, there are other considerations which support the conclusion just arrived at. These are (1) the method of origin of the secondary lamellae; (2) the lack of fundamental elements in the trama; and (3) the freedom of the primary and secondary lamellae, under normal conditions, from each other, during all stages of development.

ORIGIN OF SECONDARY LAMELLAE.—By "secondary" lamellae is meant those which arise later than the primary or first lamellae. The secondary lamellae are the shorter ones which are inserted in the space formed by the divergence of the primary ones as they extend farther from the stem. Because of the centrifugal growth and organization of the pileus, young hymenophore, and gill origins, by which the younger, or later, origins of these morphological elements appear successively in a centrifugal direction, and thus farther and farther from the stem, it will be seen that the secondary and later lamellae originate later than the primary ones, provided they are appreciably shorter than the latter. In comparatively young basidiocarps cross-sections of the hymenophore with young lamellae usually show that the secondary lamellae are narrower throughout their entire length than the primary lamellae. Some of them later become connected with the stem, while others do not.

A series of tangential sections perpendicular to the lamellae and parallel with the axis of the stem, in a comparatively young basidiocarp, the knife traveling away from the stem toward the margin of the pileus, will show the origin and different stages of development of a secondary lamella. The ends of the secondary lamellae toward the stem are arrested in development because the space is here more cramped than farther away where the primary lamellae are farther apart. Figs. 56–61 are from 6 such serial sections. A "landmark," or indicator, was selected, so that in making the photomicrographs the two primary lamellae between which

the secondary one arises could be readily located. The landmark selected is at the right in fig. 56, where there is a primary lamella and at its left a secondary one quite well developed but close to it. Following this in the successive figures up to fig. 61, it will be seen that the two become closer and closer, until both have the same trama at their junction with the pileus and appear like a double lamella, since in this region the secondary lamella evidently sprouted out of the base of the primary one. Now the area which we wish to observe for the origin of a secondary lamella, as the primary ones diverge more and more, is between the second and third primary lamella to the left of this "double" lamella. This space is between the two primary lamellae at the left of the figure. The secondary lamella originates as a salient from the palisade layer of the hymenophore between the two primary lamellae. In fig. 57 this space is broader. In fig. 58 there is seen a slight salient, some of the marginal cells of which have swollen into cystidia. Then in figs. 59, 60, and 61 it is more and more pronounced, showing the same features as the primary lamellae, but is much narrower, and because of the greater width of the primary lamellae its margin is held away from the fundamental plectenchyma below, except in figs. 60 and 61, where it is coming in contact with a few loose threads.

THE LACK OF FUNDAMENTAL PLECTENCHYMA IN THE TRAMA OF THE LAMELLAE.—If the lamellae originated as described for *C. micaceus* (LEVINE **22**), by the splitting of primary structures which form a series of radiating ridges isolated by fundamental plectenchyma or elements, then, as the approximate halves of two adjacent ridges turn toward each other to form a lamella, they would inclose some of these fundamental elements between the pileus trama and the trama of the lamella. There would be small islands of fundamental plectenchyma extending along the entire length in the base of each lamella. This is not the case. On the other hand, all the evidence goes to show that the trama is newly formed tissue and grows downward from the trama of the pileus into the lamella, and this is evident from the earliest origin of the first salients or ridges, the trama lying in the ridges, not between them. For this reason we may find, when we come to study carefully the origin of the lamellae in *Amanita* and *Amanitopsis*, that the *method of origin* is not

so very different from that presented by what I have spoken of as the *Agaricus* type. The trama of the gills suggests that the primordial trabeculae, which have thus far been the earliest observed structures, in the differentiation of the hymenophore, may originate as parallel, closely approximated thin areas of hyphal growth which remain very closely side by side until the sharper differentiation in the hymenophore appears with the formation of the palisade layers.

THE PRIMARY AND SECONDARY LAMELLAE ARE FREE THROUGHOUT THEIR DEVELOPMENT, UNDER NORMAL CONDITIONS.—If in the origin of the lamellae they were preceded by a series of isolated radial ridges with intervening areas of fundamental elements, the fundamental plectenchyma, or elements, would be continuous around these isolated ridges. Then in the later formation of the lamellae, by the splitting and parting of these ridges, tangential sections parallel with the axis of the stem would show the "trama" of the forming secondary lamellae continuous with that of the adjacent primary lamellae, as well as with the stem, until a stage of development was reached in which these connections were torn free. Such a condition is never found in normally developed plants. The secondary lamellae are free from the primary ones in all stages of development where the lamellae are normal. It not infrequently happens that the tramae of two adjacent lamellae are connected at or near the pileus, as when a secondary lamella sprouts out from the side of the base of a slightly older lamella, as shown in fig. 60, instead of sprouting out midway between two adjacent lamellae. But in these cases, also, there is no communication between the tramae of adjacent secondary and primary lamellae through their margins, as there would be at certain stages of their development if the lamellae originated as described by LEVINE.

ATTACHMENT OF THE LAMELLAE TO THE STEM.—The attachment of the lamellae to the stem in *C. micaceus* takes place in very much the same manner as described for *C. atramentarius*. The variation in details can be ascribed to specific differences. At the early origin of the lamellae the margin of the salients in cross-sections may be entirely free, or may be connected by isolated hyphae, or loose strands, across the weak annular gill activity, with the fundamental plectenchyma below on the surface of the stem, as previously

described. A spreading or fan-tailing of the margins of the lamellae immediately takes place, largely due to a swelling of the marginal palisade into cystidia-like structures. It is this fan-tailing of the gills, accompanied by the swelling of the marginal palisade cells of the young salients into cystidia-like structures, which leads to the situation observed by LEVINE (**22**, p. 351) in his fig. 8, of which he says that the palisade cells do not inclose the edge of a gill, but form an arched palisade layer in each "gill chamber" (**22**, p. 356). Exactly such a situation is shown in figs. 56–63 of the present article. The palisade layer no longer is present over the margins of these gills because at an early stage of the gill origins the palisade cells inclosing the edges of the salients become swollen into cystidia. Figs. 8, 13, and 14 of LEVINE'S paper represent quite old stages in the development of the gills.

Because of the weak annular gill cavity, the broadening of the lamellae by growth soon brings them in closer contact with the stem, or the rather thin layer of fundamental plectenchyma which clothes the stem. Because of the loose and shredded character of this fundamental plectenchyma, the loose hyphae readily interlock with the swollen marginal cells of the lamellae, and with isolated hyphae which grow down from the marginal trama of the lamellae. The frazzled layer of fundamental plectenchyma on the surface of the stem is much thinner in *C. micaceus* than in *C. atramentarius*. For this reason the round or angular cells of the stem surface very soon come in contact with the trama of the lamellae as the surface cells are spread laterally by the increasing pressure of contact. There is, therefore, a wedging together, to a greater or less extent, of the trama and stem cells which often presents the appearance of pseudoparenchyma. The different stages are represented in figs. 55–63 and 65–67.

The attachment of the lamellae to the stem, therefore, is a gradual process, proceeding from the young to the older stages of the lamellae and basidiocarp. It is interesting to note that LEVINE'S fig. 8 represents the weak annular gill cavity, below the margins of the gills, which are loosely connected by isolated hyphae or loose strands extending across the cavity to the stem, or the layer of fundamental plectenchyma on its surface. It represents very

much the same situation as is presented by my fig. 50, except that the latter is nearer the stem, so that a few of the lamellae in the middle of the figure are in close contact with the stem. If the gills originated as described by LEVINE, then they could remain firmly connected with the stem until in age they become free with the expansion of the plant. They would not show during the young stage the loose connection across a weak, general annular gill cavity which is evident from his fig. 8. In fig. 51 the elements of the margins of the primary lamellae are interlocking with the fundamental plectenchyma on the stem surface, better shown in figs. 56–63, more highly magnified. The later stages are shown in figs. 65–67. Fig. 64 is from a section of the entire fruit body at quite an advanced stage of development, when the gills are finally firmly connected with the surface of the stem. The stem here shows a number of lysigenous cavities. Figs. 66 and 67, more highly magnified, from the same basidiocarp, show the close connection of the trama with the stem.

Summary

1. GENERAL ORGANIZATION OF THE BASIDIOCARP.—In the young basidiocarps the pileus is organized in the region of the convergence of radially growing hyphae which arise from the apex of the basidiocarp fundament. The primordium of the pileus also grows in a radial direction, both upward and in a lateral and slightly downward direction, over the broad and nearly horizontal surface of the young stem fundament. The growth of the pileus is more rapid in the lateral centrifugal direction, and the hyphae here are richer in protoplasmic content. The zone of radial hyphae enveloping the pileus is the blematogen. In *Coprinus comatus* and *C. atramentarius* the radial hyphae of the blematogen layer retain their filamentous character and the blematogen is persistent, being concrete with the pileus, and therefore does not separate as a distinct volva or teleoblem. In *C. micaceus* the radial hyphae of the blematogen change at a very early period into branched chains of oval and globose cells. Profuse disarticulation of the chains takes place, forming a somewhat powdery material on the surface of the pileus. The outer surface layer of the pileus forms a

distinct palisade zone of cells which at maturity become so compactly crowded together that any remaining slender supporting hyphae of the chains of rounded cells are pinched off. The blematogen in *C. micaceus*, therefore, becomes free from the pileus in the form of mica-like flakes, which are easily removed; but the blematogen is set free in a different manner from the cleavage process occurring in species of *Amanita* and *Amanitopsis* which have been studied with respect to this feature. In *C. micaceus* the outer surface of the pileus remains intact, and the blematogen is freed by scaling off, or "desquamation" as interpreted by DEBARY.

2. THE GENERAL, ANNULAR, PRELAMELLAR CAVITY is formed by a tearing apart of the fundamental plectenchyma in the angle between the pileus and stem fundaments, due to tension resulting from differences in rapidity of growth. For this reason the tissue surrounding the cavity is at first more or less shredded. The cavity is relatively large in *C. comatus*, and weak or very weak in *C. atramentarius* and *C. micaceus*. In the two latter species, during the tearing or shredding of the fundamental plectenchyma, isolated hyphae or loose strands of a few hyphae extend across the cavity here and there because of its weakness.

3. THE PALISADE LAYER OF THE YOUNG HYMENOPHORE begins its formation near, at, or upon the apex of the stem, and then proceeds outward in a centrifugal direction over the under surface of the pileus, following the centrifugal growth of the latter. In *C. comatus* the palisade layer begins some distance from the apex of the stem, since there is a circular sterile area on the under surface of the pileus next to the stem. In *C. atramentarius* and *C. micaceus* it begins at the apex of the stem fundament and then proceeds outward in a centrifugal manner. In some cases it extends a short distance down the surface of the stem apex. In these species it may be organized before or at the time of the formation of the weak gill cavity.

4. THE LAMELLAE ORIGINATE AS DOWNWARD PROJECTING SALIENTS of the palisade hymenophore fundament, in a series radiating outward toward the margin of the pileus, the younger portions of the salients being toward the margin of the pileus and continuing

to arise in a centrifugal direction, following up the progressive development in the same direction of the palisade hymenophore, cavity, and pileus margin. The salients are formed by increase and enlargement of the elements of the palisade layer along these radial areas and by the downward growth of the subadjacent trama cells of the pileus. The lamellae increase in width by apical and also by intercalary growth.

5. THE ATTACHMENT OF THE GILL MARGINS TO THE STEM takes place after the origin of the gills. It begins when the gill margins come in contact with the stem, or the fundamental plectenchyma surrounding the stem. The age and breadth of the lamellae when the attachment begins varies in the different species and in different individuals, according to the strength of the general gill cavity and the proximity of the gill to the margin of the nearly mature pileus, where the space may be more cramped.

In *Coprinus comatus* the lamellae may become quite broad before they begin their attachment, except at the extreme margin of the pileus. Before they begin to form the attachment with the stem, the palisade layer is continuous over the margin, the palisade cells here not being differentiated from those on the sides. After they have been in contact with the stem surface for some time many of the marginal cells are spread laterally by the pressure. Others, together with short hypha from the end of the trama, interlace lightly with the open meshed plectenchyma on the surface of the stem.

In *Coprinus atramentarius*, since the general gill cavity is weak, the young salients, as well as the intervening spaces, are connected here and there by isolated hyphae, or loose hyphal strands which were not ruptured during the tearing apart of the fundamental plectenchyma below the young hymenophore palisade. The palisade layer extends over the margin of the young salients. As the lamellae broaden, the margins press against and into the loose ragged surface of the fundamental plectenchyma on the surface of the stem. Short slender threads from the margins grow outward and interlock with this fundamental plectenchyma. As the pressure becomes greater, many of the palisade cells are pressed laterally so that there is a partial connection of the trama ends with

the fundamental plectenchyma on the surface of the stem. Since the gill origins are more or less adnate to the stem in different individuals, sections parallel with the axis of the stem and passing through these origins on the apex of the stem, in the angle between pileus and stem, may lead to error in the interpretation of the gill origins, since the trama, arising here from the stem as well as from the pileus, is attached to both. The sections then present pockets or "stalls," with the palisade layer converging toward their centers. As soon as the sections pass beyond the portions arising from the stem apex, the relation of the gills to the pileus presents the normal appearance.

In *Coprinus micaceus*, because of the weak, general gill cavity, isolated hyphae and loose strands remain attached here and there, not only to the gill origins but to the portion of the hymenophore between them in the early stages of the salients, or gill origins. The palisade layer of the hymenophore is continuous over their margins, but very soon the marginal cells swell into globose or broadly clavate cystidia, and by the crowding of these cells the margins of the gills spread laterally, or fan-tail. The protoplasmic content in the marginal cells being thus diluted, the margin of the gill does not stain deeply. The gill margins soon press against the thin layer of fundamental plectenchyma on the surface of the stem. There is an interlocking of hyphae and also an interwedging of the marginal cells of the gills and trama with the surface cells of the stem.

6. THE CYSTIDIA have not been thoroughly examined in this study, since they did not come within the limits of the special problem undertaken at this time. Furthermore, their thorough study would require examination also of material in the fresh condition, at the time of the separation of the gills from the stem. But it has been observed that many at least of the cystidia in *Coprinus atramentarius* arise from cells of the trama beneath the subhymenium.

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EXPLANATION OF PLATES V–XII

Pl. VI is not reduced; the other plates are reduced as follows: pl. VII to $\frac{10}{11}$ of the diameter of the photomicrographs; pls. IX, X, and XI to $\frac{2}{3}$; pls. V, VIII, and XII to $\frac{5}{7}$. Magnifications are given in connection with descriptions of figures. The photomicrographs were made by the author, 9 of them with Spencer Lens Co. 16 mm. photo lens and Zeiss camera, the remainder with Zeiss microscope and Leitz simple camera stand.

PLATES V–VII

FIGS. 1–25.—*Coprinus comatus.*

FIG. 1.—One side of section of upper end of young basidiocarp before formation of annular gill cavity and young hymenophore; constriction at right indicates delimitation of pileus and stem; no internal differentiation apparent, but radiating system of threads marks blematogen; ×30.

FIG. 2.—Another basidiocarp representing an older stage, the section being median or nearly so, and parallel with axis of stem; annular cavity, therefore, present in section as two cavities, one on each side of stem; deeply staining tissue above cavity is young hymenophore before formation of palisade layer; *p*, pileus; *b*, blematogen; ×30.

FIG. 3.—Tangential section from same basidiocarp in which annular gill cavity shows as a transversely elongated opening a few threads of the shredded tissue extending across; ×30.

FIG. 4.—Tangential section of another basidiocarp parallel with axis of stem; annular gill cavity showing as transversely elongated cavity; palisade layer not yet formed over any portion of surface, and surface still in frazzled condition, resulting from tearing apart of fundamental plectenchyma; fundament of hymenophore indicated by more deeply staining tissue above at each side; ×50.

FIG. 5.—Left side of fig. 4 more highly magnified; ×80.

FIG. 6.—Still more highly magnified detail of frazzled roof of cavity in another section from same plant; loose hyphae of fundamental plectenchyma below; ×500.

FIG. 7.—One side of median longitudinal section of a basidiocarp in which palisade layer is forming; blematogen at right; young palisade hymenophore above annular gill cavity; ×50.

FIG. 8.—Same from another section slightly more magnified; a few threads from shredded tissue extending across cavity; young hymenophore above; dark area at right represents surface of pileus, with blematogen at its right; ×80.

FIG. 9.—Tangential and longitudinal section of same basidiocarp just passing out of stem surface with some frazzled fundamental plectenchyma on

surface of stem showing in middle portion; young hymenophore palisade above on each side; ×50.

FIG. 10.—Tangential section of same basidiocarp, but farther from stem, showing young hymenophore palisade above; ×135.

FIGS. 11–16.—Longitudinal sections of another basidiocarp, parallel with stem axis; see text diagrams for position of sections.

FIG. 11.—One side of median section showing large annular gill cavity; roof at right (next stem) sterile; over center the primordia of lamellae forming (details shown in figs. 13–16); left of center young hymenophore palisade which also extends downward; *p*, pileus; *b*, blematogen; ×45.

FIG. 12.—Tangential section through palisade portion beyond gill salients, that is, toward margin of pileus; by their radial or centrifugal growth gill salients would later push down from this palisade; ×45.

FIG. 13.—Tangential section nearer stem, showing over middle portion cross-sections of young gill salients; on each side palisade layer, farther from stem, over which gill salients appear later; ×45.

FIG. 14.—Tangential section still nearer stem; gill salients over middle portion less prominent than those on each side; section passing through them at point where they originate just beyond sterile area next stem; toward margin of pileus on each side is young hymenophore palisade; ×45.

FIG. 15.—Tangential section still nearer stem, middle portion passing through sterile area; on each side, farther from stem, young gill salients, and nearer margin of pileus young hymenophore palisade; ×45.

FIG. 16.—Portion of tangential section near that of fig. 13 showing details, on one side, of young hymenophore palisade and young gill salients; ×160.

FIG. 17.—Median longitudinal section of another and slightly older basidiocarp, somewhat tangential to middle line, so that young gill salients are cut somewhat obliquely; note large gill cavity; *p*, pileus; *b*, blematogen; ×50.

FIG. 18.—Tangential section of same beyond stem, showing cross-section of young gill salients; ×35.

FIG. 19.—Portion of still older basidiocarp, nearly transverse to stem, showing at one side transition from gill salients to young hymenophore palisade and frazzled stage of young hymenophore next margin of pileus; note palisade layer extending over margin of gill salients as it does in all younger stages; ×200.

FIGS. 20–22.—Tangential sections parallel with axis of stem, but through curvature of pileus, and "back" or dorsum of the gills, lateral portion of pileus at this stage being nearly parallel with stem, the margin curved inward by epinasty; in fig. 20 section is nearer stem, so that middle gills are free at lower extremity; in figs. 20 and 22, successively nearer pileus, all gills are cut through dorsal portion; ×40.

FIGS. 23, 24.—Sections nearly transverse to stem of basidiocarp, showing method of attachment of margin of gills to stem; pressure of margin of gills against stem, or fundamental plectenchyma on its surface, presses some marginally palisade cells laterally, while others, as well as some trama cells,

interlock with open mesh of stem surface or covering; in fig. 24 one gill has slightly withdrawn; ×300.

FIG. 25.—Portion of section from nearly mature basidiocarp showing attachment (below) of gill margins to stem; ×35.

PLATES VIII AND IX

FIGS. 26–45.—*Coprinus atramentarius.*

FIG. 26.—Slightly oblique section through stem and pileus at stage of young hymenophore palisade, showing weak general annular gill cavity on each side; blematogen very distinctly marked off from pileus; in this basidiocarp surface of young hymenophore rises at oblique angle from axis of stem; ×40.

FIG. 27.—Median longitudinal section showing weak general annular gill cavity; *p*, pileus; *b*, blematogen; ×70.

FIG. 28.—Tangential section of same, showing gill origins on this side of plant; ×70.

FIG. 29.—Same plant, but section on other side of stem where hymenophore is younger and in palisade stage; note weak gill cavity; ×70.

FIG. 30.—Same but tangential section through surface of stem; ×70.

FIG. 31.—Same plant; section entirely tangential, showing hymenophore palisade at left, and very slight gill origins at right; ×70.

FIG. 32.—Same section more highly magnified; ×115.

FIG. 33.—Tangential section of younger basidiocarp, showing weak general annular gill cavity with shredded fundamental plectenchyma, some hyphae extending across to young hymenophore palisade; ×700.

FIG. 34.—Portion at left of fig. 32 more highly magnified to show details of palisade layer, etc.; note the three very slight salients, fundaments of lamellae arising by pushing down of palisade cells by elongation of subadjacent trama hyphae; note weak general gill cavity and loose threads of torn fundamental plectenchyma extending across indefinitely to young palisade salients and to palisade portions between them; ×400.

FIG. 35.—Portion of same still more highly magnified, showing single palisade gill salient with even palisade portion of young hymenophore on either side; ×700.

FIG. 36.—Section slightly oblique to axis of stem, but tangential and perpendicular to surface of young hymenophore which rises at angle (as in fig. 26), but more highly magnified; note weak gill cavity and shredded fundamental plectenchyma; ×105.

FIG. 37.—Another section of same basidiocarp, but close to stem, showing slight gill salients (over middle portion) which are very broad, as origins extend part way down on stem as in species with adnate or adnexed gills; ×105.

FIG. 38.—Tangential section, but parallel with axis of stem, showing margins of gills beginning attachment to stem; note distinctness of pileus and blematogen zones; ×40.

FIG. 39.—Tangential section close to stem; middle lamellae well attached to stem, because space in angle between pileus and stem is less than at greater

distance, and also because of adnate or adnexed gills the salients arise from upper part of stem as well as from pileus; ×40.

FIG. 40.—Tangential section, very close to stem, of a basidiocarp with adnate gills; over middle portion the dark bars are gill origins attached to stem as well as to pileus, that is, they grew out from upper surface of stem as well as downward from pileus; farther toward margin of pileus the margins of gills are just beginning attachment to stem surface; ×40.

FIG. 41.—Section transverse to stem of older basidiocarp, showing method of attachment of gill margins to stem; note interlocking of marginal cells of gills with loose fundamental plectenchyma on stem; ×215.

FIG. 42.—Slightly older stage, also transverse to stem, showing interlocking of marginal cells and fundamental plectenchyma on stem surface; note numerous cystidia on sides of gills; ×215.

FIG. 43.—Older stage; section transverse to stem; margins of gills well attached; note rather broad zone of fundamental plectenchyma between gill margins and distinctive stem tissue; ×215.

FIG. 44.—Still older stage; section transverse to axis of stem; paraffin ribbon slightly overheated to cause gills to separate from stem; note gills bound closely together by hymenial surfaces; in one gill original palisade cells still extend over margin; in others they are spread laterally; portions of fundamental plectenchyma cling to gill margins; broad zone of fundamental plectenchyma on distinctive stem surface; ×215.

FIG. 45.—Portion from same ribbon not overheated; note hymenial surfaces (deeply stained) closely joined; loose mesh of trama; in center large cystidium which arises from middle of trama and projects into hymenium of adjacent gill; ×215.

PLATES X–XII

FIGS. 46–71.—*Coprinus micaceus.*

FIG. 46.—Section of young basidiocarp parallel with axes of stem and nearly median, showing weak annular gill cavity; very distinct blematogen zone external to pileus; ×105.

FIG. 47.—Same, but section near surface of stem, showing very young lamellae cut obliquely; general gill cavity below margin of salients, some of latter still connected with a few loose threads of fundamental plectenchyma; ×105.

FIG. 48.—Median longitudinal section of slightly older basidiocarp; section between gills on each side so that cavity appears larger; ×65.

FIG. 49.—Section of same basidiocarp and near that shown in fig. 48, but through gills on each side so that full width of gills is shown; weak general annular cavity between margin of gills and surface of stem, with scattered threads of shredded fundamental plectenchyma extending across cavity; in figs. 48 and 49 note blematogen zone enveloping pileus and stem; ×65.

FIG. 50.—Tangential section of same basidiocarp just in angle where stem and pileus join; gills in middle adnate to stem, giving appearance of margins

firmly attached to stem; on each side a few scattered threads of torn fundamental plectenchyma extending across weak general annular gill cavity and connected with margins of gills; ×65.

FIG. 51.—Tangential section of another basidiocarp; gills beginning their attachment to stem; ×65.

FIGS. 52–55.—Serial tangential sections of a young basidiocarp, from near margin of pileus toward stem; weak general annular gill cavity; shredded fundamental plectenchyma below, torn in formation of cavity; fig. 52, near margin of pileus, shows young hymenophore palisade above cavity forming an even layer; in fig. 53 weak salients are fundaments of lamellae; these more pronounced in fig. 54; in figs. 53 and 54 note palisade layer continuous over margins of gill salients; a few scattered hyphae of fundamental plectenchyma extend across to salients and also to palisade layer between; in fig. 55 gill salients more pronounced and at this young stage marginal palisade cells swelling to form cystidia; in figs. 53–55 note lighter color of trama tissue where it is pushing down as trama of gills, due to elongation of cells; ×400.

FIG. 56–63.—Tangential sections parallel with axis of stem and perpendicular to pileus and lamellae, showing independent origin of a secondary lamellae (figs. 56–61) rising between two primary lamellae at left; cells on margins of secondary lamellae also swell into cystidia; in all figures cystidia on margins of gills as well as for some distance back; note elongation of cells in trama of lamellae and subadjacent tissue of pileus with decrease in absorption of stain, due to the growth by elongation which pushes gill fundaments down from even palisade layer of young hymenophore; cells of gill margins interlock with frazzled fundamental plectenchyma on surface of stem; ×400.

FIGS. 64–67.—Further stages in attachment of gills to stem.

FIG. 65.—Rounded edges of gills crowding into thin zone of loose fundamental plectenchyma on surface of stem; cells interlocking and interwedging; ×230.

FIGS. 64, 66, 67.—Transverse section of nearly mature basidiocarp; fig. 64, arrangement of gills and their complete attachment to surface of stems; lysigenous cavities in stem; depressions ("striae") above primary gills; ×30; figs. 66 and 67, details of union of gill margins and stem surface; ×230.

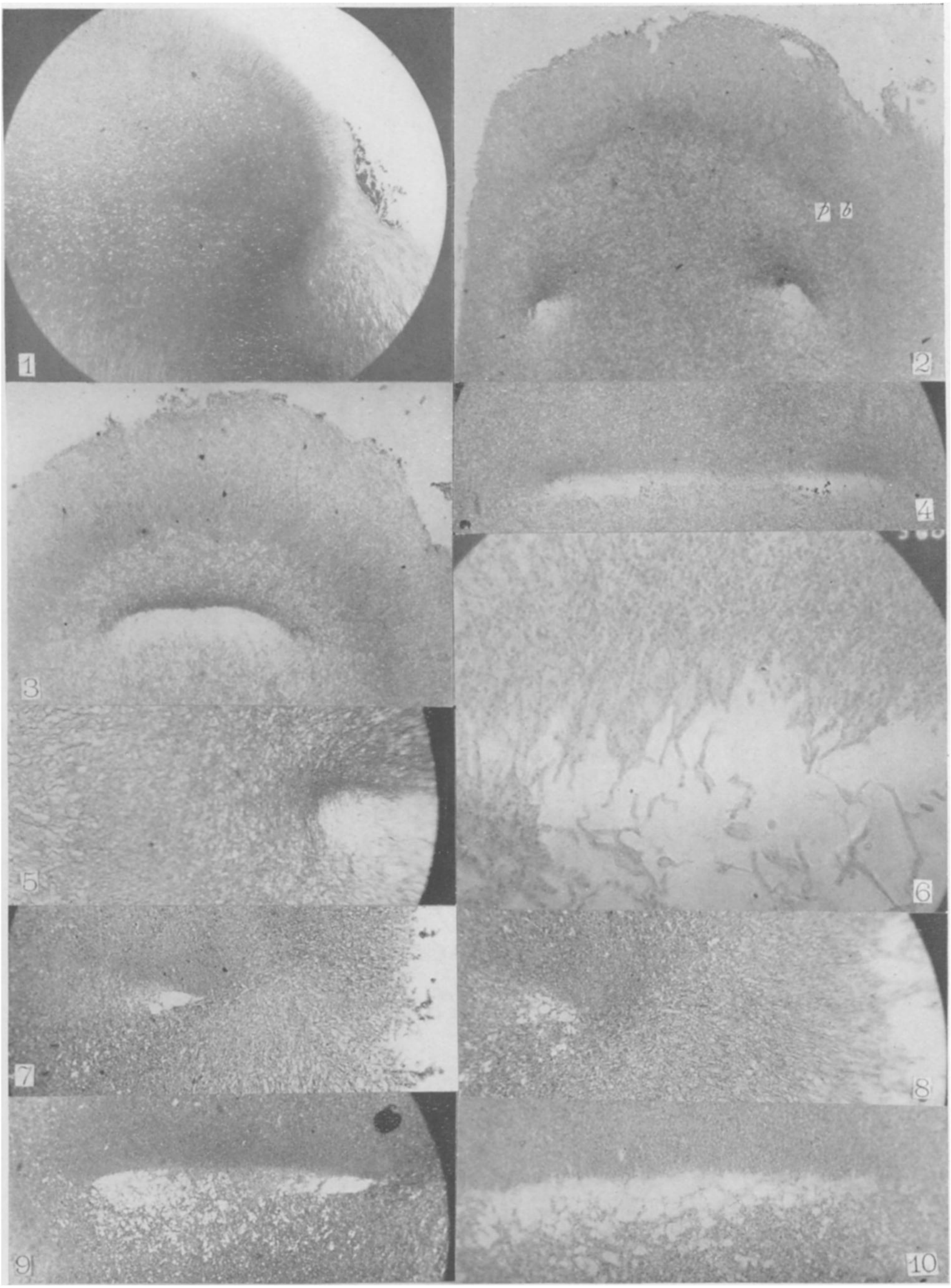
FIGS. 68–71.—Organization of palisade layer on surface of pileus.

FIG. 68.—Surface of young pileus marked by irregular threads projecting a short distance in large-celled zone of blematogen.

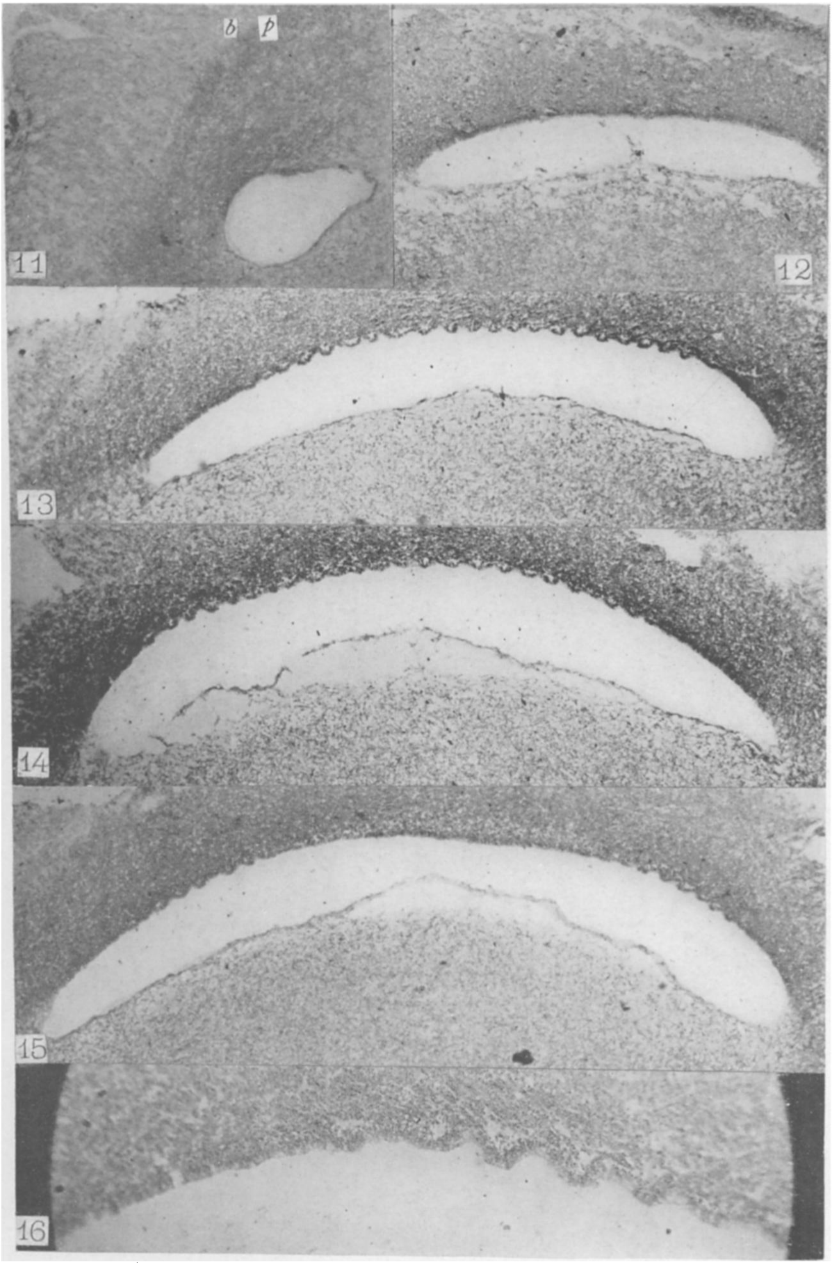
FIG. 69.—Slightly older stage, showing more compact arrangement of surface elements of pileus.

FIG. 70.—Still older stage, showing distinct but rather irregular palisade zone forming surface of pileus next blematogen zone.

FIG. 71.—Nearly mature plant (same as fig. 64), showing details of pileus structure in transverse section; very distinct and well organized palisade layer of surface; note indentations (cross-section of "striae"); blematogen entirely shed by desquamation.



ATKINSON on COPRINUS COMATUS



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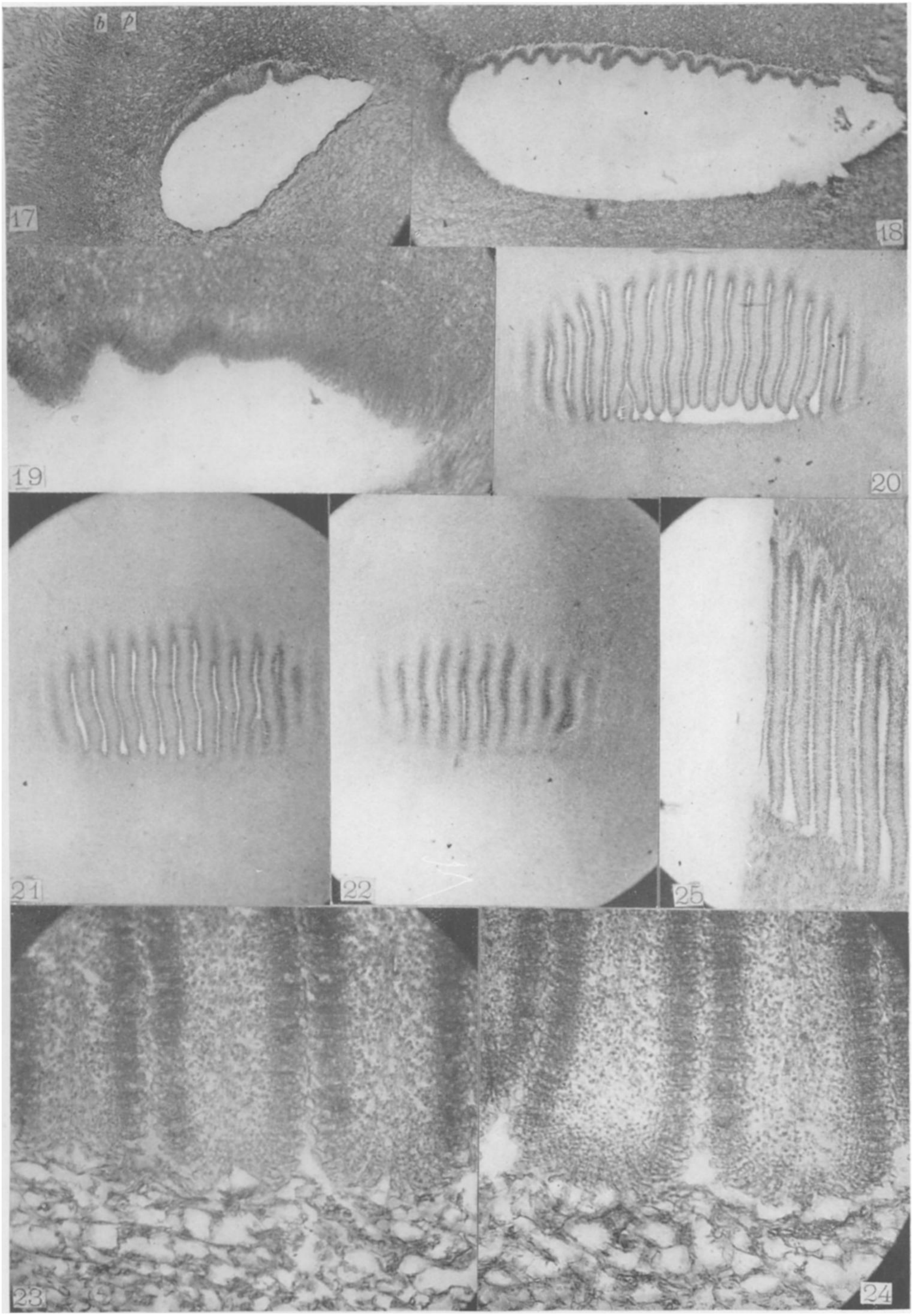

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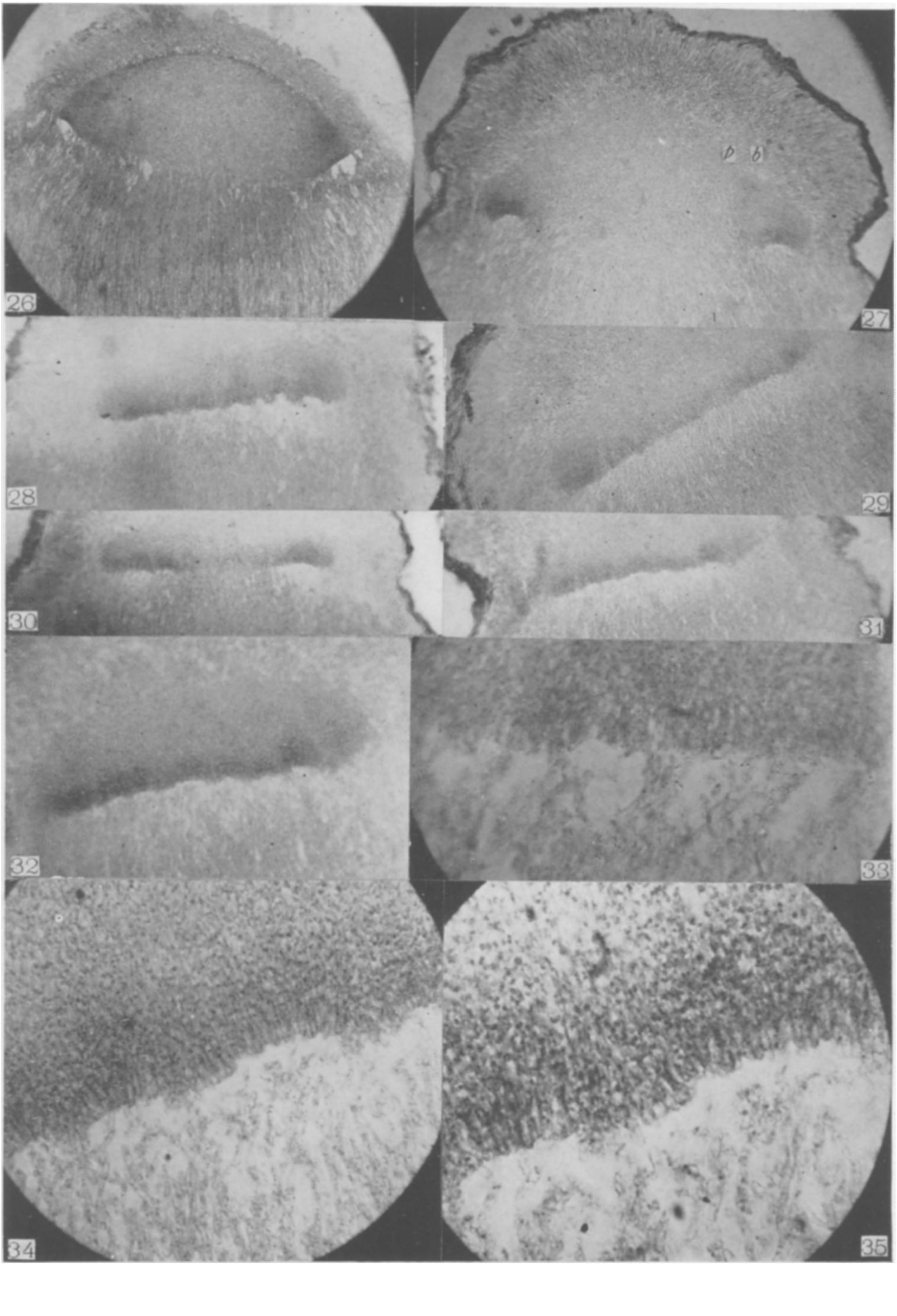
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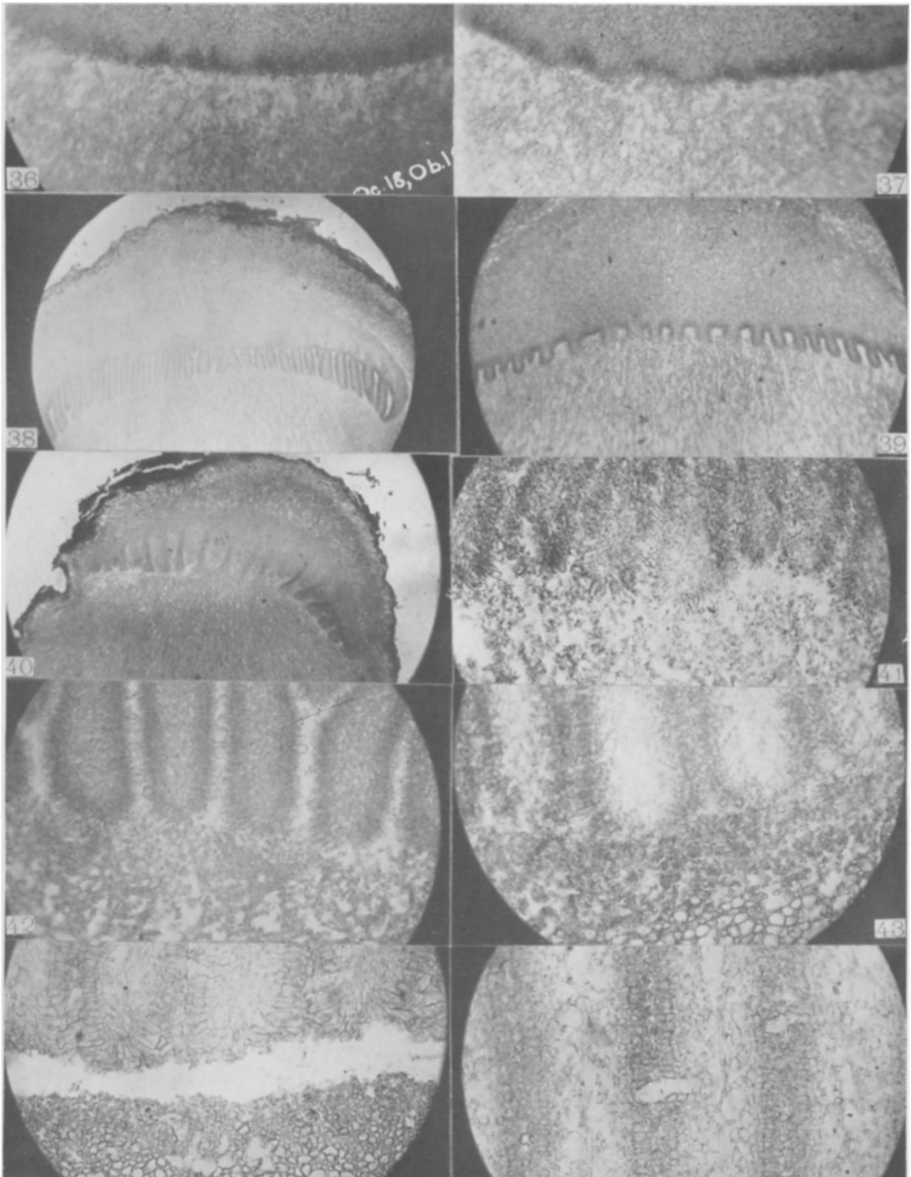
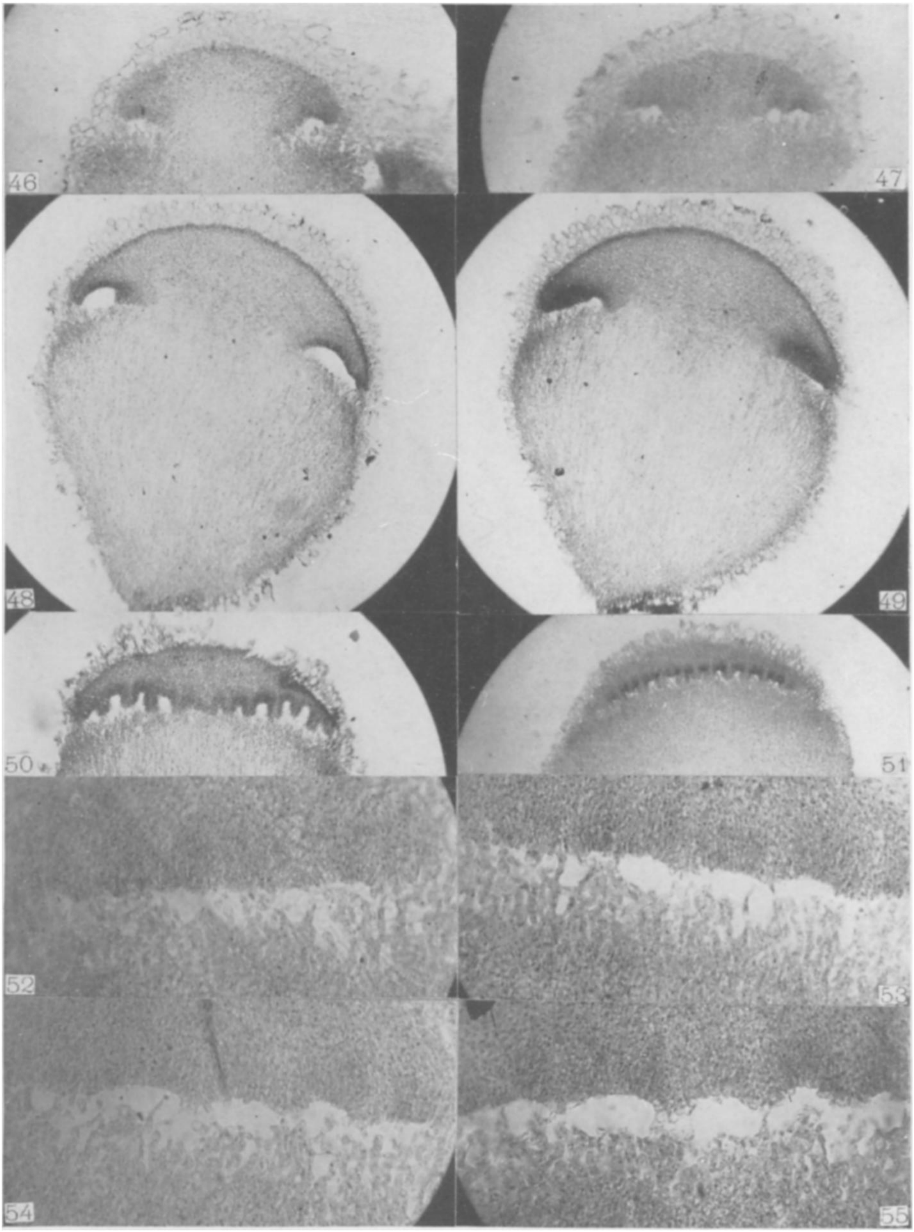
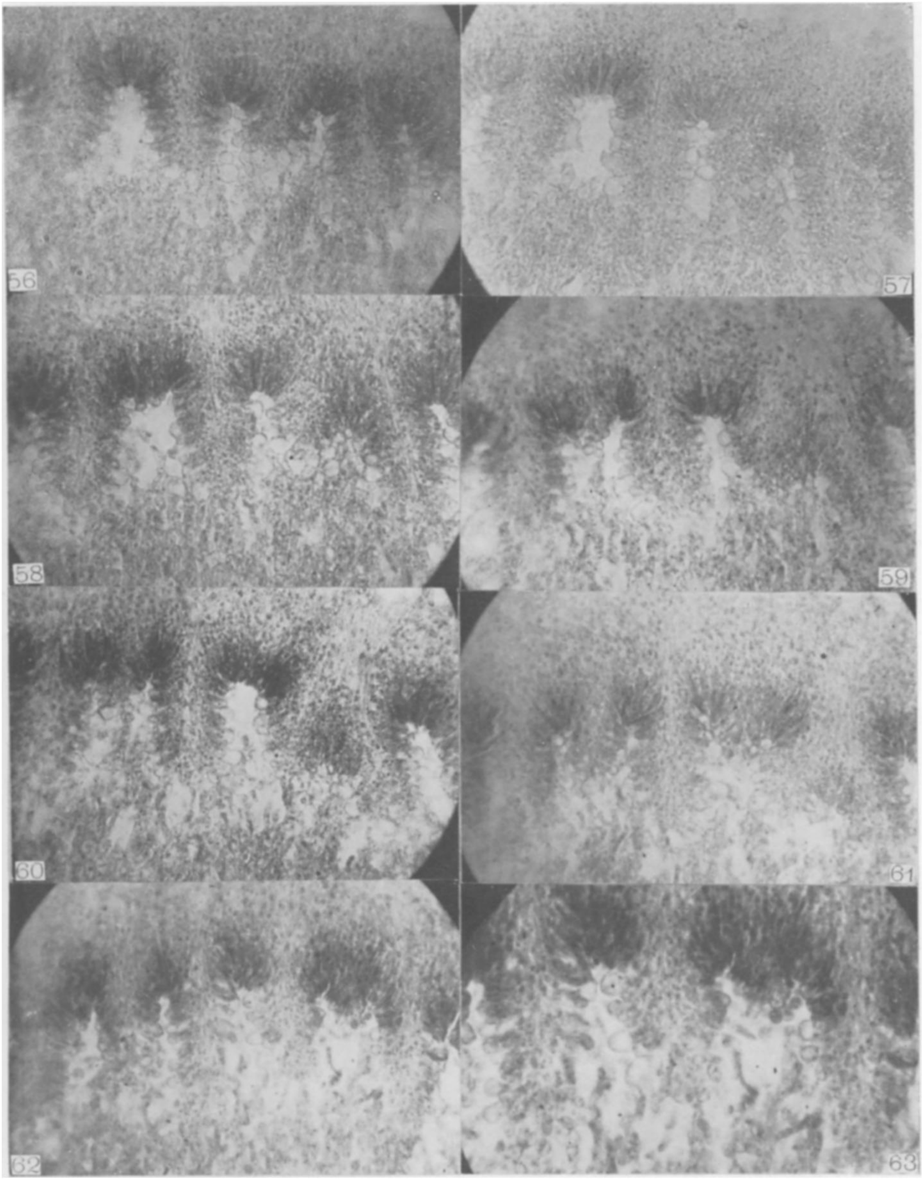


ATKINSON on COPRINUS ATRAMENTARIUS



ATKINSON on COPRINUS MICACEUS



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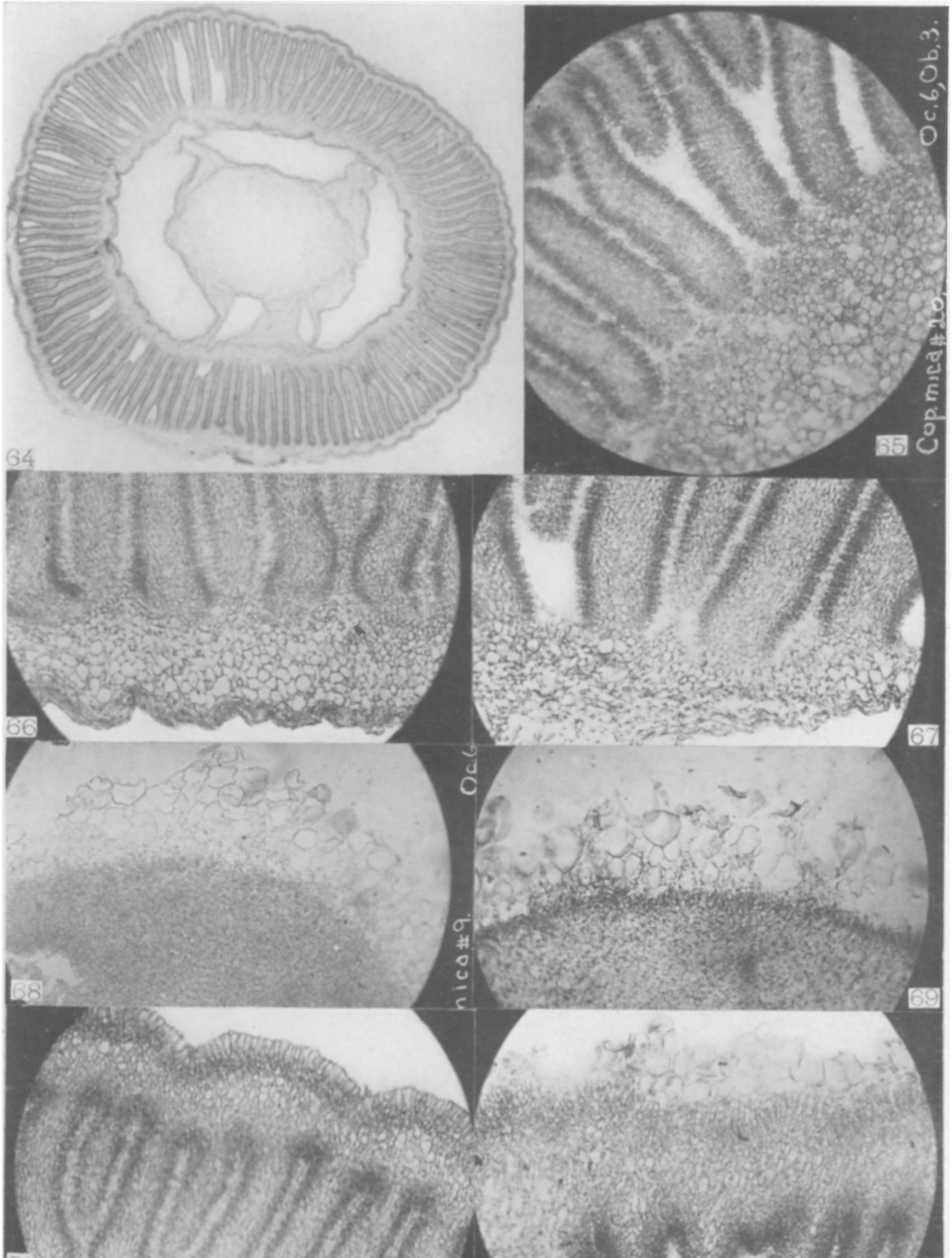

ATKINSON on COPRINUS MICACEUS